REVISION OF THE GENUS PONTEDERIA L.

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This small group of emersed aquatics is comprised of five species which are distributed throughout the tropical, subtropical and temperate regions of the New World. The center of diversity of *Pontederia* occurs in Middle America where the two recognized subgenera perhaps originated. A similar morphology, geography, cytology and chemistry suggest that *Reussia* Endl. does not warrant generic status apart from *Pontederia*. Subgeneric status is selected for *Reussia* since the species comprise a natural but distinct phyletic unit within *Pontederia*

Pontederia is quite variable in habit and leaf shape. Individual species, *i.e. Pontederia cordata* L., have many leaf forms which have contributed to the creation of many unwarranted taxa and combinations in the past. This is partly attributed to the limited geographical scopes of previous taxonomic studies of the genus. It has been important to recognize that distinct species have a development of similar leaf polymorphisms throughout a wide geographical range. Also where it has been possible, floral and fruit characters are selected to elucidate the natural phyletic units that comprise *Pontederia.*

NOMENCLATURAL HISTORY

Over two centuries ago Linnaeus (1737a, b, 1754) described the genus *Pontederia.* More than a few attempts have been made to clarify the typification of the genus. In order to elucidate the past (and consequently the present) status of *Pontederia* it is necessary to examine the following chronology of historical events:

Linnaeus (1737a) — Synonymy of Morison as communicated by Gronovius is cited along with the generic description of *Pontederia,* translated as follows:
calyx: Spathe common, oblong, laterally dehiscing.
corolla: Connate, biparted, gaping. Upper lip erect, flat,

of 3 equal parts. Lower lip reflexed, 3 parted, segments equal.

stamens: Filaments 6, awl-shaped, of which [1 stamen] is situated on each segment of the lower lip of the fused corolla, the 3 remaining [stamens] are closed under the upper lip.

pistil: Ovary not completely rounded. Style simple, short. Stigma undivided.

perigone: Capsule [little box or encasement] ovate [inside], 3 compartments, 3-valved, 3-angled, 3-furrowed.

seeds: Not completely rounded, many.

Linnaeus (1737b) — Dedication of the genus to Julio Pontedera, with special reference to the American Pickerelweed, Maryland and Virginia, of Morison, Petiver and Plukenet. The genus *Carimgolo* of Malabar was mentioned.

Linnaeus (1753) — Three species of *Pontederia* were enumerated in the class *Hexandria:* (1) *P. ovata,* with ovate foliage, flowers in heads, *Narukila* of Rheed. mal., habitat Malabar; (2) *P. cordata,* with cordate foliage, flowers in spikes, with identical reference made of the *Hortus Cliffortianus*, habitat Virginia; (3) *P. hastata,* with foliage hastate, flowers in umbels, *Carimgola* of Rheed. mal., habitat India.

Linnaeus (1754) — Generic description is the same as that in the first edition (1737) except for the following additions (translated):

corolla: tubular.

stamens: inserted on corolla, of which 3 are awl-shaped, long, and inserted on the throat of the corolla tube; 3 remaining stamens attached at the base of the same tube. Anthers pointed inwards.

pistil: Ovary oblong, above receptacle. Style simple, *very short,* curved downwards.

perigone: Capsule [encasement] fleshy, conic, apex wide and bent inwards.

Adanson (1763) — *Narukila* was listed with reference to *Pontederia* L. [*Narukila* is a nomen confusum.]

Rafinesque (1808, 1830) — Established the genus *Unisema* from that element of *Pontederia* described by Linnaeus (1753) as *P. cordata*. ". . . L. [Linnaeus] positively says that the fruit of it [*Pontederia*] is *3 locular and many seeded* [Linnaeus; 1737a, 1754]. I observed . . . the singular one seeded fruit [of *P. cordata*] and established the genus [*Unisema*] . . ."

Farwell (1924, 1928) — "As defined by Linnaeus in the Genera [1754], this genus is restricted to his *P. hastata*, the only species named by him in the *Species Plantarum* that had a many-seeded, 3-celled capsule, as was pointed out by Rafinesque . . ."

Sprague (1924) — *Carimgola* (Linnaeus, 1737b) was not definitely cited as a synonym of *Pontederia* since locality, the Maryland and Virginia habitat, and synonymy references (Linnaeus, 1737 a,b) are of *P. cordata*. "Thus it is evident that in 1737 he [Linnaeus] gave the new generic name *Pontederia* to the species subsequently named by him *P. cordata*, and that he was uncertain whether *Carimgola* (*P. hastata*) was congeneric or not."

Fernald (1925) — "The description of the genus *Pontederia* in the 5th edition of the *Genera Plantarum* (1754) was a mixture based upon the 2nd and 3rd species of the *Species Plantarum;* but in general the name has been maintained by post-Linnaean botanists for the American *Pontederia cordata;* Linnaeus's 1st species, *P. ovata* ['a plant with 1 stamen'], clearly not belonging in the class *Hexandria*, being excluded as a member of the family Marantaceae, and the 3rd species, *P. hastata*, separated off as *Monochoria* Presl." ". . . in the 1st edition of the *Genera*, Linnaeus [1737a] gave the same mixed description as in the 5th [1754], the capsules 3-valved and many-seeded, but stated that the plant was communicated by Gronovius (from Virginia)."

It is apparent from his three species that Linnaeus (1753) accidentally assembled dissimilar taxa under *Pontederia*. Farwell (1924) and Fernald (1925) point out that *P. ovata* having 1 stamen obviously did not belong in the class *Hexandria* which includes *P. cordata* and *P. hastata.* Taxonomists must examine more critically the 1st and 5th editions of the *Genera Plantarum* (Linnaeus; 1737a, 1754) to know if Linnaeus (1753) actually considered *P. cordata* or *P. hastata* as the "type" of the genus.

Rafinesque (1808, 1830) insisted that the genus *Pontederia* as described by Linnaeus (1737a, 1754) called for fruits "3 locular and many seeded." Thus, Rafinesque established his genus *Unisema* from the Linnaean *P. cordata* having 1-seeded fruits. Farwell (1924, 1928) adopted Rafinesque's decision.

Sprague (1924) and Fernald (1925) defended *P. cordata* as the intended "type" of the Linnaean *Pontederia* based on locality (the Maryland and Virginia habitat) and synonomy (Morison, Petiver, Plukenet and Gronovius) as presented by Linnaeus (1737 a,b, 1753, 1754). Fernald (1925) also appealed to established custom which until today treats *P. hastata* as the Asian *Monochoria* and *P. cordata* as the American *Pontederia.* This appeal has been enforced by "principal systematic botanists" such as, Pursh (1814), Nuttall (1818), Torrey (1824), Solms-Laubach (1883), Britton and Brown (1913), Sprague (1924), Fernald (1925), Schwartz (1927), Hitchcock and Green (1929), and Castellanos (1951). All have retained and reinstated *Pontederia cordata* L. as the type of the Linnaean *Pontederia.*

The interpretation by Rafinesque (1808, 1830) of the Linnaean generic description of *Pontederia* (1737a, 1754) was accepted beyond doubt by Sprague (1924) and Fernald (1925). Fernald openly admitted Rafinesque's interpretation that the *Genera Plantarum* (1737a, 1754) called for "capsules 3-valved and many-seeded" and therefore Linnaeus based his generic description on a mixture of the 2nd (*P. cordata*) and 3rd (*P. hastata*) species of the *Species Plantarum* (1753). Both Sprague and Fernald sought valid evidence (locality and synonomy) in the *Genera Plantarum* (1737a, 1754) for support of *P. cordata* as "type" ignoring the generic description of the

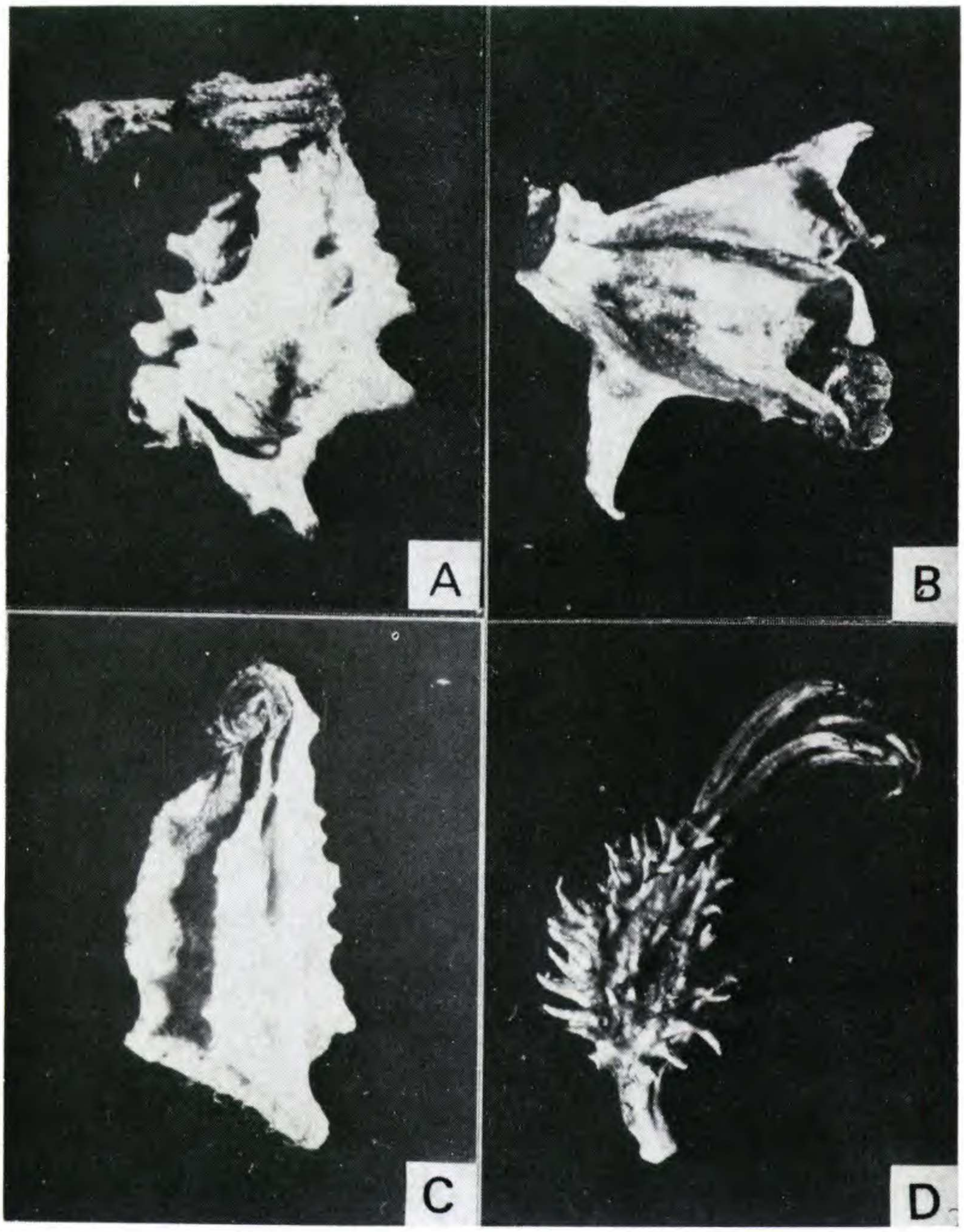

Figure 1. Hardened Perigone Bases of *Pontederia*. A. Tooth-ridged perigone of *P. cordata* var. *cordata*, U.S., Ohio (*Lowden*, 36, 37), 8 mm long. B. Smooth-ridged perigone of *P. sagittata*, Mexico (*Lowden* 6), 8 mm long. C. Tooth-ridged perigone of *P. parviflora*, Panama (*Lowden* 21), 8 mm long. D. Spinulose-ridged perigone of *P. rotundifolia*, Nicaragua (*Lowden* 17, 18), 10 mm long.

Linnaean protologue and the fact that it was misinterpreted by Rafinesque.

Rafinesque (1808, 1830) confused the modern terminology of "capsules 3-loculed and many seeded" (which actually applies to *P. hastata*) with the Linnaean choice of terminology in the *Genera Plantarum*. Linnaeus (1737a, 1754) used "capsula" to mean a "small box" or "encasement" and it was properly identified by him as part of the perigone (perianth). In general appearance the mature perigone of *P. cordata* (Fig. 1A) is triangular in all aspects and is rounded inside. Linnaeus never stated as Rafinesque insisted that the fruits were very many seeded, he only stated there were many seeds which implies without assumption each plant or inflorescence bears many seeds. This as does the rest of the generic description of the *Genera Plantarum* (1737a, 1754) fits perfectly *P. cordata* and can not be confused with the Asian *P. hastata* (*Monochoria hastata*). *Pontederia hastata*, with flowers actinomorphic, petals nearly free to the base (corolla not tubular), stamens 6 of which 1 is longer and seeds round, *can not possibly* be confused with the Linnaean *P. cordata*, with flowers zygomorphic, perianth 2-lipped, petals connate (tubular), stamens 6 of which 3 are longer and seeds not completely rounded. The additional wording of the 5th edition of the *Genera Plantarum* (1754) reveals that Linnaeus was describing the short style floral form (Fig. 3A, 3 stamens longer and a *very short* style) of tristylous *P. cordata*. The perigone encasement (capsule) was accurately described as fleshy, conic, with apex (Fig. 1A, mature stamens and upper portion of perigone) wide and bent inwards.

The Linnaean generic description of *Pontederia* (1737a, 1754) is exclusively that of *P. cordata* and not *P. hastata*. Linnaeus (1753) was sure of the morphological structure of *P. cordata* as it was explicitly expressed by him in the *Genera Plantarum*. Linnaeus accidentally included *P. ovata* and *P. hastata* in the *Species Plantarum* (1753) as he accidentally mentioned *Carimgolo* (= *P. hastata*) in his

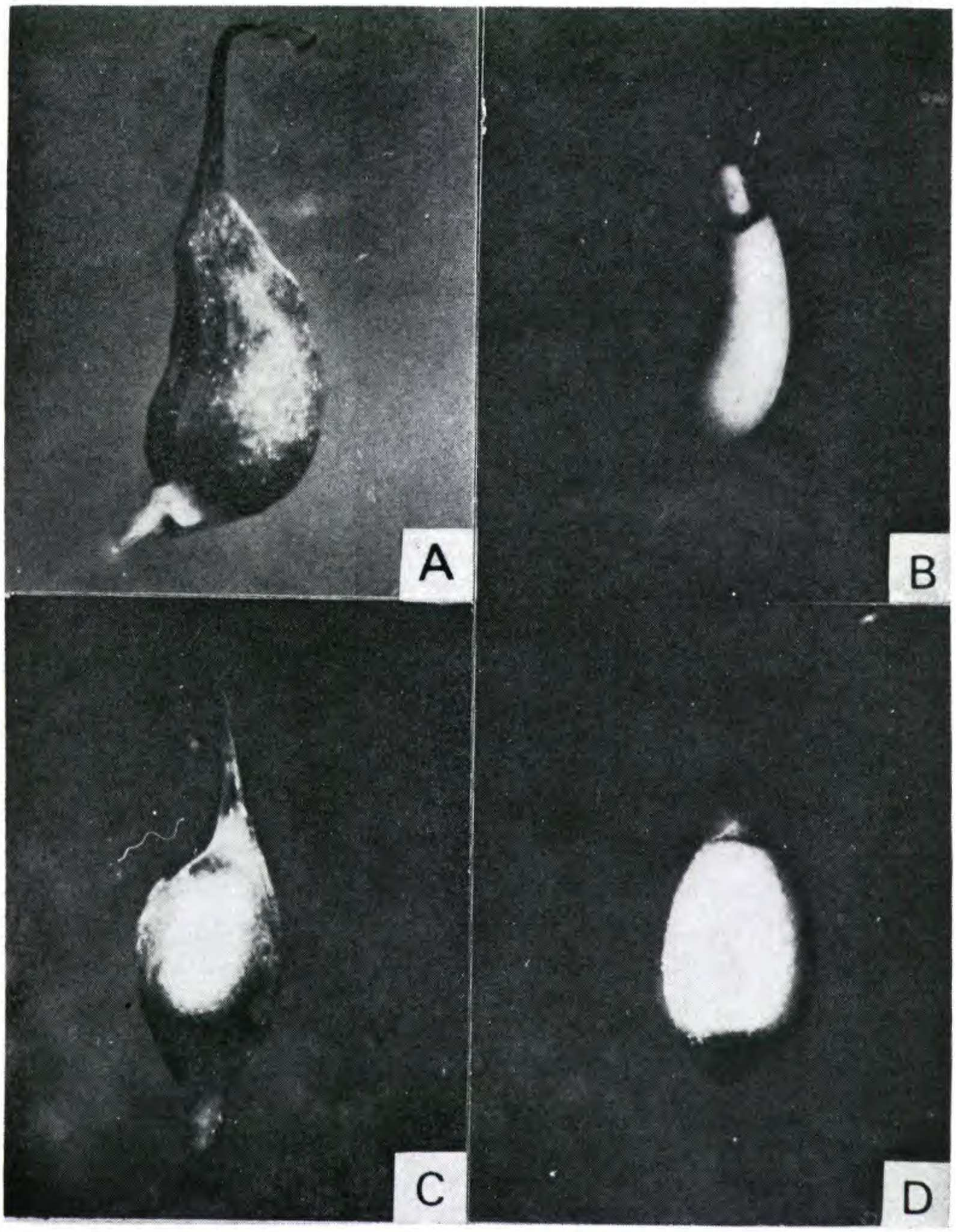

Figure 2. Fruits and Seeds of *Pontederia*. A. Utricle of *P. parviflora*, Panama (*Lowden* 21), 8.5 mm long. B. Portion of copious endosperm surrounding embryo of *P. parviflora*, Panama (*Lowden* 21), 4 mm long. C. Utricle of *P. rotundifolia*, Nicaragua (*Lowden* 17, 18), 8.5 mm long. D. Ovoid seed of *P. rotundifolia*, Nicaragua (*Lowden* 17, 18), 3 mm long.

Hortus Cliffortianus (1737b). It is difficult to understand why Linnaeus mentioned these taxa (perhaps they appeared superficially similar), since he made no mention of them in the generic description of the *Genera Plantarum.* This revision adopts *Pontederia cordata* L. as the lectotype of the Linnaean *Pontederia.*

In Solms-Laubach's treatment (1883) of the Pontederiaceae, *Pontederia* L. was recognized as being generally distinct from *Reussia* Endl. Both have one-seeded indehiscent fruits and two-lipped perigones (perianth). *Pontederia* was characterized by having 3 lobes in each lip, whereas, *Reussia* was characterized by having 5 lobes in the upper lip and 1 lobe in the lower lip. This was followed by Schwartz (1927, 1930), Schulz (1942) and Castellanos (1951, 1958). In accordance with this distinction, Castellanos (1951) transferred *Pontederia rotundifolia* L. f. to *Reussia* based on his reported observation of 5 lobes in the upper lip of the perigone.

My observations indicate that *Pontederia* species including *P. rotundifolia* have 3 lobes in each lip, even though the deepest incisions of the perigone occur on both sides of the smallest lobe of the lower lip. Contrary to later opinions, Endlicher (1836) described *Reussia* as having 4 lobes in the upper lip and 2 lobes in the lower lip. Certainly, the number of lobes in each lip is a confused and weak distinction for separating *Pontederia* and *Reussia.* Additional evidence obtained in the present investigation indicates that *Pontederia* and *Reussia* are so morphologically, cytologically and chemically similar as to warrant the treatment of *Reussia* (nom. cons.) as a subgenus of *Pontederia* in accordance with the *International Code* (1972, Appendix III, p. 284 and Article 14).

DISPERSAL MECHANISMS

Pontederia inhabits inland fresh waters and marshes transitional to salt waters along the coasts. It is primarily a genus of tropical and subtropical America, whose habitats are probably held in check by latitude (temperature) and altitude (elevation). Mountain ranges, as exemplified by the Appalachian (Core, 1966) and Rocky Mountains in North America, the Sierras Madre Oriental and Occidental in Mexico, Sierras del Mico and Minas in Guatemala, Mayan Mountains in Guatemala and British Honduras, Cordillera Isabelia in Honduras, Cordillera de Talamanca in Costa Rica and the Andes in South America have been natural physiographic barriers promoting the speciation of *Pontederia* in the Americas. Geographical isolation is greatest among taxa within Middle America such as, *P. sagittata* (Fig. 16) and *P. parviflora* (Fig. 19).

Dispersal by water of *Pontederia* utricles is thought to be the main mode of long range dispersal, with vegetative reproduction a prominent factor in population establishment. The utricle is buoyant and consequently its distribution is due to the light aeriferous tissue of the perigone base (Fig. 1) surrounding it. Schulz (1942) reports a flotaion period longer than fifteen days for seeds enclosed in perigone bases which is long enough for the fruit to travel a considerable distance. The presence of fleshy perigone bases surrounding the utricles and the copious endosperm contained inside (Fig. 2B) greatly increase survival expectancy over long distances traveled.

Long distant dispersal of utricles (Fig. 2A, C) by avian and terrestrial animals (Sculthorpe, 1967) is considered to be of less frequent occurrence. Field observations of *Pontederia rotundifolia* at the Laguna Zapotitan, Dept. La Liberatad, El Salvador and in the fields of Lago Arenal, Province Guanacaste, Costa Rica suggest limited local terrestrial dispersal by animals. Both areas are inhabited by livestock on which the spinulose perigone bases (Fig. 1D) are easily anchored.

Vegetative reproduction by trailing prostrate branched stems and by rhizomes is of frequent occurrence throughout populations. Clones are recognized by clumping of plants within populations (Fig. 9). Rhizome fragmentation results in the establishment of new clones within close proximity. Field observations indicate that the prostrate branched stems of *P. rotundifolia* with adventitious roots at each node may easily become severed and rooted. Trailing stems and rhizomes are able to survive harsh environmental pressures as organs of food accumulation during the climatic fluctuations of temperate and tropical regions.

TRISTYLY

Tristyly, as the term relates to *Pontederia*, is the type of heterostyly in which three kinds of plants occur in a species. These are (1) plants with flowers having a SHORT STYLE, 3 medium stamens and 3 long stamens (Sml); (2) plants with flowers having 3 short stamens, a MEDIUM STYLE and 3 long stamens (sMl); and (3) plants with flowers having 3 short stamens, 3 medium stamens and a LONG STYLE (smL. The Sml, sMl and smL floral forms (Fig. 3A-C) were found in *Pontederia cordata* (including varieties), *P. sagittata*, *P. rotundifolia* and *P. subovata*. Only *P. parviflora* has plants with 3 short stamens, 3 long stamens and a LONG STYLE (slL). The slL floral form (Fig. 3D) is an excellent diagnostic character for distinguishing this homostylous taxon from its closely related tristylous counterparts of subgenus *Pontederia*.

Legitimate pollinations (Fig. 4, pollen transfer from a stamen to the stigmatic surface of a pistil of equivalent length) are more productive of seeds than illegitimate pollinations (Fig. 4, pollen transfer from a stamen to the stigmatic surface of a pistil not the equivalent length). Ornduff (1966) demonstrated with *Pontederia cordata* that self-incompatibility (self and own-form pollinations are illegitimate) is "considerably stronger" in the smL and Sml floral forms than in the sMl floral form. Regarding legitimate pollinations the sMl floral form had a greater percentage seed production than the smL and Sml floral forms.

An indication of this breeding system of individual populations may be extrapolated through the study of the frequency of floral forms within populations of different *Pontederia* taxa (Table 1). In populations where all three

Table 1. Floral Form Frequency in Pontederia based on Population and Herbarium Studies[1]

Taxon	Populations & Vouchers	# (%) Inflorescences Sml	sMl	smL	slL
P. cordata var. *cordata*	U.S. Ohio, Ottawa Co., Winous Pt. SW of Port Clinton, *Lowden* 36 & 37.	8(33.3)	5(20.8)	11(45.8)	—
	British Honduras. Belize District: 9 miles N of Belize City, *Lowden* 24;	5(62.5)	2(25.0)	1(12.5)	—
	29 miles N of Belize City, Cowhead Creek, *Lowden* 26;	0(0)	0(0)	3(100)	—
	32 miles N of Belize City, *Lowden* 27;	2(66.7)	1(33.3)	0(0)	—
	Hattieville Burrell Boom Road, 5½ miles from Burrell Boom, *Lowden* 28.	0(0)	2(40.0)	3(60.0)	—
var. *lancifolia*	U.S. Florida, Holmes Co., 0.2 miles E of Florida 81 in Ponce de Leon, *Stone* 2589 Sml, 2590 smL & 2591 sMl.	+	+	+	—
var. *ovalis*	Brazil. Mato Grosso, 300 km. past Cuiaba in route to Goiania, *Maguire et al* 56931 Sml; Brasilia,	+	+	+	—

[1]Code to floral forms: (Sml) SHORT STYLE, 3 medium stamens, 3 long stamens; (sMl) 3 short stamens, MEDIUM STYLE, 3 long stamens; (smL) 3 short stamens, 3 medium stamens, LONG STYLE; (slL) 3 short stamens, 3 long stamens, LONG STYLE. A plus sign (+) indicates the occurrence of the floral form, whereas a dash (—) indicates the floral form is unknown in the taxon.

Table 1. (cont.)

Taxon	Populations & Vouchers	# (%) Inflorescences			
		Sml	sMl	smL	slL
	Federal District, *Prance & Silva* 59082 smL. Colombia, Dept. Boyaca, near Orocue, *Haught* 2716 sMl.				
P. sagittata	Mexico. State Vera Cruz: Vera Cruz, El Coyol, *Lowden* 6;	46 (33.8)	52 (38.2)	38 (27.9)	—
	El Puente de Teculapilla, Carretera Nacional 180, 5 km. NW of Lerdo, *Lowden* 7;	5 (55.6)	1 (11.1)	3 (33.3)	—
	Laguna Catemaco, Arroyo Agrio, *Lowden* 9.	10 (76.9)	3 (23.0)	0 (0)	—
	Guatemala. Dept. Izabal: Quirigua, *Lowden* 10;	2 (9.1)	12 (54.5)	8 (36.4)	—
	Puerto Barrios, *Lowden* 11	10 (32.3)	14 (45.2)	7 (22.2)	—
	Honduras. Dept. Cortes: Puerto Cortes, *Lowden* 13;	0 (0)	6 (37.5)	10 (62.5)	—
	13.5 miles inland from Puerto Cortes, *Lowden* 14.	16 (47.1)	7 (20.6)	11 (32.3)	—
	Dept. Atlantida: Tela, La Curva, *Lowden* 15;	15 (34.1)	16 (36.4)	13 (29.5)	—
	Santiago, 11 miles W of Tela, *Lowden* 16.	21 (55.3)	12 (31.6)	5 (13.2)	—
P. parviflora	Panama. Province Herrera, Los Llanos de Santa Maria, *Lowden* 20;	—	—	—	89 (100)

Table 1. (cont.)

Taxon	Populations & Vouchers	# (%) Inflorescences Sml	sMl	smL	slL
	Province Panama, between Pacora and Chepo, *Lowden* 21;	—	—	—	83(100)
	17 herbarium specimens cited under specimens examined.	—	—	—	+
P. rotundifolia	El Salvador. Dept. La Libertad, Laguna Zapotitan, *Lowden* 23.	0(0)	0(0)	29(100)	—
	Honduras. Dept. Comayagua, Lago Yojoa, Pito Solo, *Lowden* 12.	0(0)	30(81.1)	7(18.9)	—
	Nicaragua. Dept. Granada, near Granada, *Lowden* 17, 18.	0(0)	1?(0.7?)	145(99.3)	—
	Costa Rica. Province Guanacaste, 1 km. from Arenal, 2 km. from Trenadora, *Lowden* 19.	184(100)	0(0)	0(0)	—
P. subovata	Paraguay, prope Concepcion, *Hassler* 7352 Sml; Brazil, Estado Minas, Mun. Ituiutaba, Loc. S. Terezuiha, *Marcedo* 3168 sMl; Argentina, Prov. Chaco, Lcc. Colonia Benitez, *Meyer* 3864 smL.	+	+	+	—

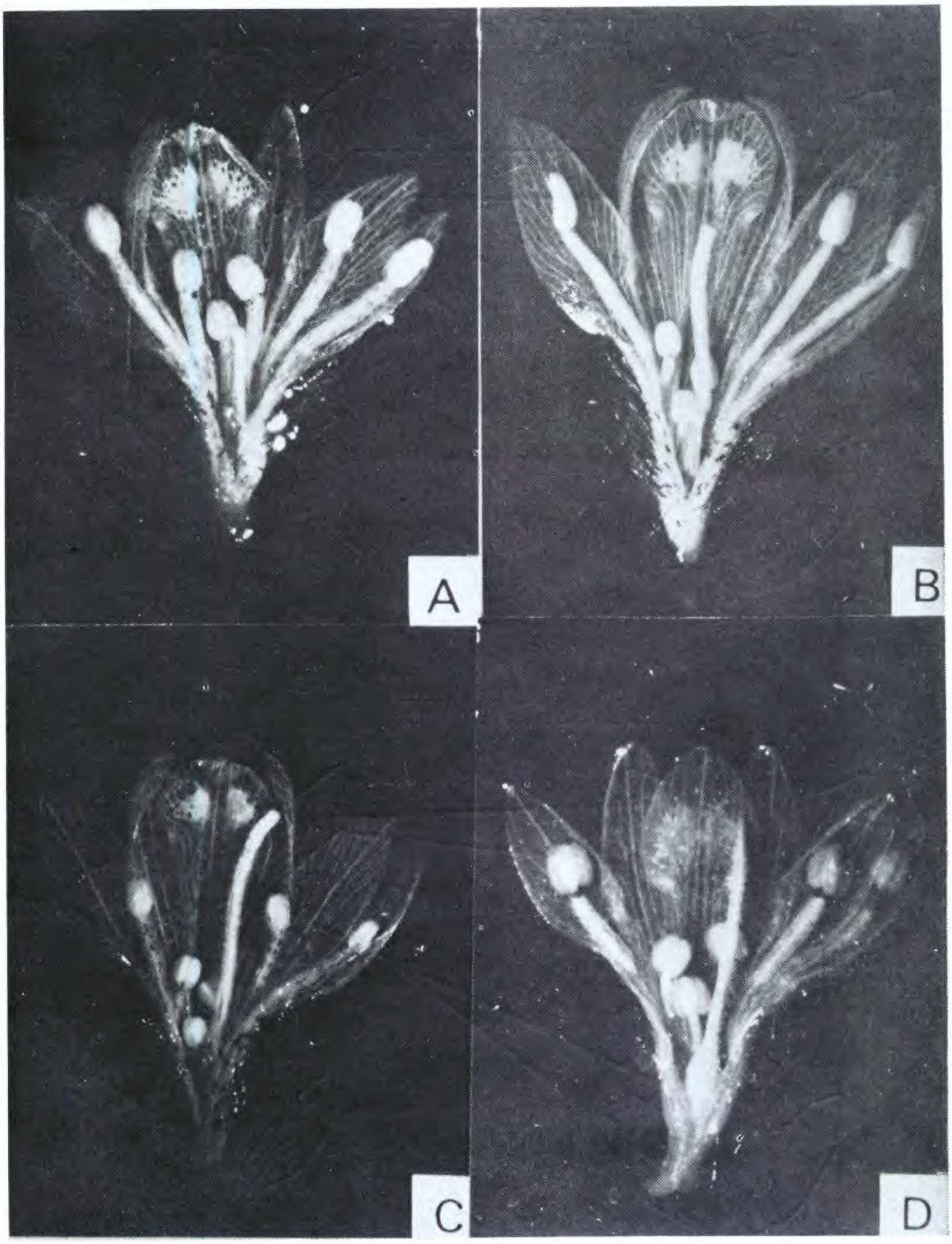

Figure 3. Floral Forms of *Pontederia*. A. SHORT STYLE, 3 medium stamens, 3 long stamens (Sml); *P. rotundifolia*, Costa Rica (*Lowden* 19), 10 mm long. B. 3 short stamens, MEDIUM STYLE, 3 long stamens (sMl); *P. rotundifolia*, Honduras (*Lowden* 12), 13 mm long. C. 3 short stamens, 3 medium stamens, LONG STYLE (smL); *P. rotundifolia*, Nicaragua (*Lowden* 17, 18), 11 mm long. D. 3 short stamens, 3 long stamens, LONG STYLE (slL); *P. parviflora*, Panama (*Lowden* 21), 7 mm long.

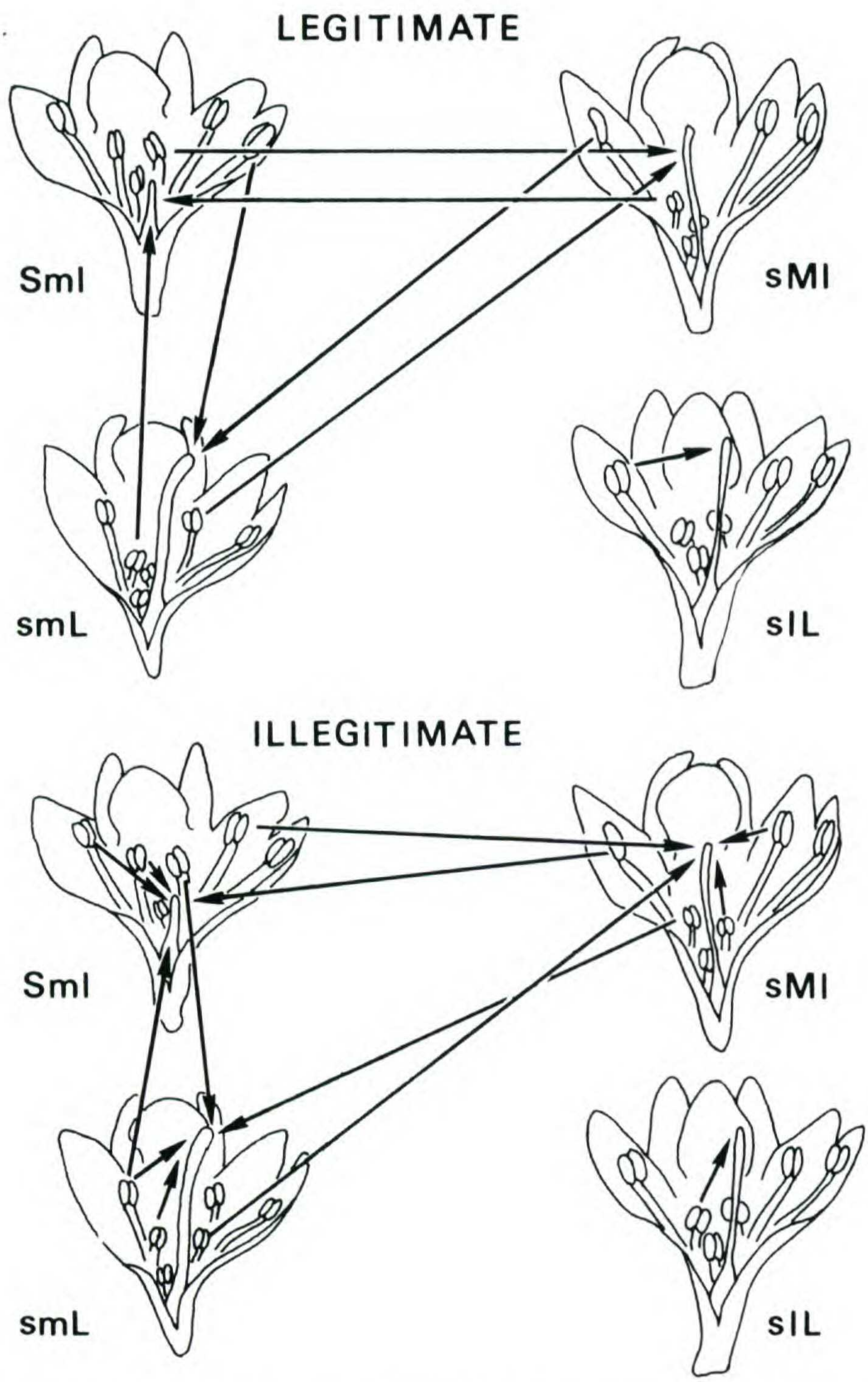

Figure 4. Legitimate and illegitimate pollinations in *Pontederia* floral forms (arrows represent the transfer of pollen from anthers to stigmas). See Fegure 3 for code to floral forms.

floral forms are present, it is difficult, only on the basis of frequency of occurrence, to know if any one floral form has greater breeding value compared with another floral form in the same population. However, in *Pontederia rotundifolia* three out of four populations examined (Table 1) had the frequent occurrence of one floral form in the absence of the other two (e.g., the smL floral form was found at Lago Nicaragua, Nicaragua and is absent at Lago Arenal, Costa Rica where the Sm1 floral form was found). These populations perhaps represent clonal establishment of a single floral form in which a certain amount of inbreeding must be occurring through illegitimate pollinations (selfing and own-form). Even though an incompatibility system is operative there is not total incompatibility in populations containing a single floral form.

The homostylous *Pontederia parviflora* has most likely been derived from a tristylous floral form. This is perhaps a step towards increased self-compatibility in one member of the genus. Field observations (in Panama) indicate a compatibility system due to the high seed set of infructescences.

In *Pontederia* a reproductive system has evolved which is highly tolerant to different pressures of the environment. Tristyly functions in juxtaposition with an effective mode of vegetative reproduction. Subgenus *Reussia* is characterized by having few flowered inflorescences (less seed production) and long trailing stems. Stem fragmentation, especially in populations having one floral form (*P. rotundifolia*), has greater immediate population survival value than reproduction through a tristylous breeding system. In subgenus *Pontederia,* inflorescences are many flowered (greater seed production), and the erect, above ground stems are much shorter. In this subgenus, tristyly perhaps has greater long range survival value and homostyly (*P. parviflora*) appears to be derived from a tristylous ancestor.

CYTOLOGICAL STUDIES

Smith (1898) recorded $n=8$ and $2n=16$ for *Pontederia*

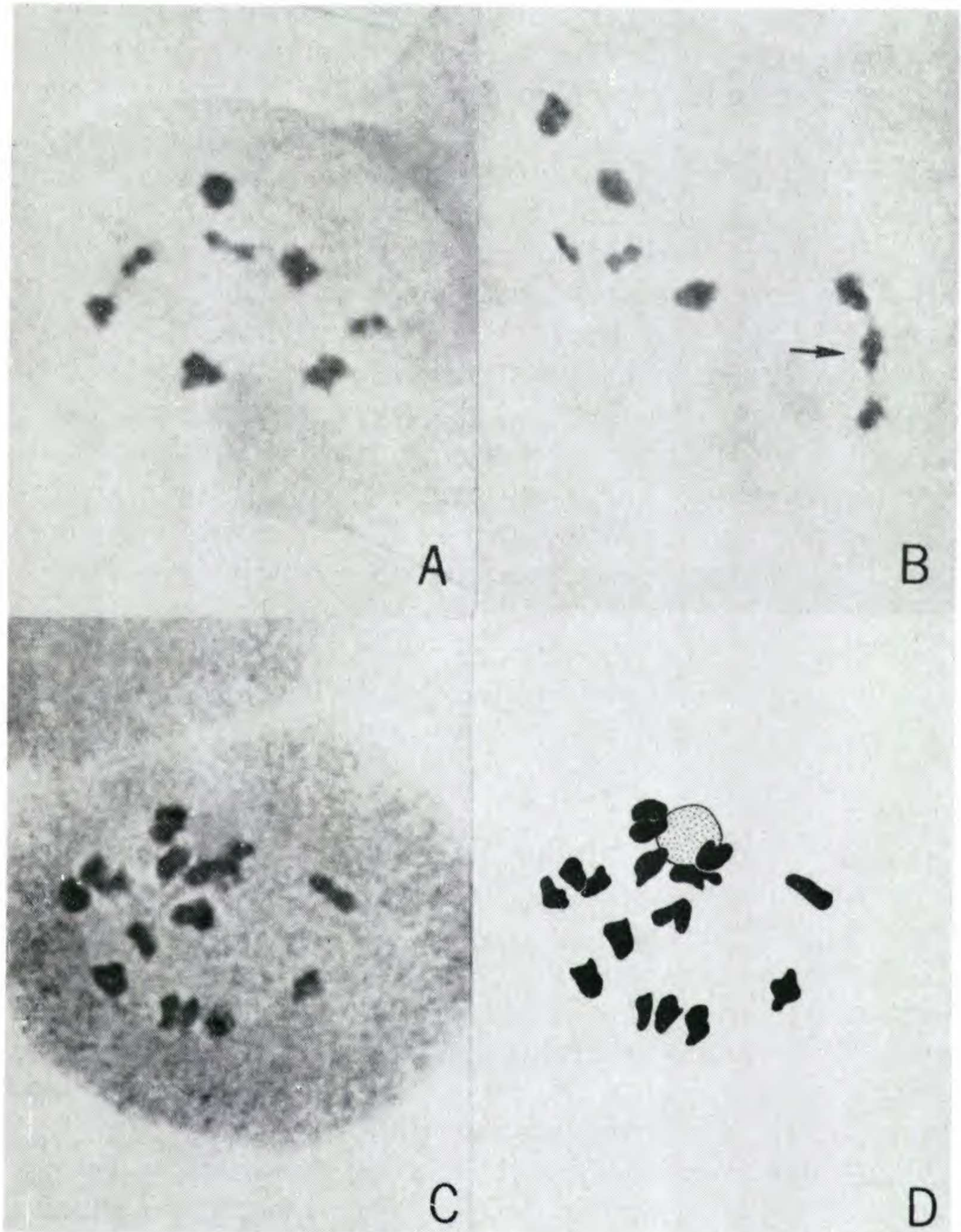

Figure 5. Chromosome Configurations in Microsporocytes of *Pontederia*. A. Eight bivalents (diakinesis) of *P. cordata* var. *cordata*, U.S., Ohio (*Lowden* 36, 37). B. Secondary association of six chromosomes (arrow points to three bivalents) of *P. cordata* var. *cordata*, U.S., Ohio (*Lowden* 36, 37). C. Sixteen bivalents of *P. rotundifolia*, Nicaragua (*Lowden* 17, 18). D. Diagramatic representation of C, showing sixteen bivalents of *P. rotundifolia*.

cordata. The cytological investigations of Bowden (1945) verified Smith's counts. This study reconfirms these earlier reports and elucidates counts (Table 2) for other *Pontederia* taxa.

Young *Pontederia* inflorescences still enclosed by the spathe and the petiole base of the flower stalk leaf were collected for microsporocytes undergoing meiosis. Inflorescences were placed in 100% ethanol and glacial acetic acid (3:1 respectively). After 24 hours, they were stored in 70% ethanol until anthers were stained with iron acetocarmine.

Microsporogenisis in taxa examined of subgenera *Pontederia* and *Reussia* is normal except for the occasional occurrence of secondary associations of either 4 or 6 chromosomes (Fig. 5B). Haploid counts (Table 2) during diakinesis (Fig. 5) indicate a base number of $x=8$ in *Pontederia.* Subgenera of *Pontederia* might be distinguished cytologically by the numbers, $n=8$ in subg. *Pontederia* and $n=16$ in subg. *Reussia.* The polyploid *P. rotundifolia* and possibly *P. subovata* (not examined) most likely evolved from an $n=8$ ancestor.

CHEMOTAXONOMIC STUDIES

Phenolic compounds, especially flavonoids, have recently been the subject of a large number of chemosystematic studies. These studies (Alston, 1967) have shown that color and position of phenolic compounds on chromatograms can be used to show systematic relationships without necessitating chemical characterization. Considering the validity of this empirical chromatographic data the following chemical studies were initiated in order to assess the degree of variation in phenolic patterns within and between taxa of *Pontederia,* to see if phenolic patterns of *Pontederia* taxa correlate with that indicated by morphology and geography, and to note if similarity in phenolic patterns exists between taxa of *Pontederia, Eichhornia* and *Heteranthera* (related genera).

The methods employed are essentially those outlined by

Mabry, Markham and Thomas (1970). Phenolic compounds were extracted from dried flower stalk leaf material in 50% aqueous-methanol for at least 24 hours before 4 ml of individual leaf extract were spotted on Whatman 3MM chromatographic paper. The two-dimensional solvent systems were: (1) 3 parts TBA : 1 part glacial acetic acid : 1 part distilled water and (2) 15% HOAc. Chromatographic patterns were read using no reagent in visible light, then in UV light with and without NH_3.

Twenty-six principal spots (Fig. 6) were discernible by position and color on chromatograms. Color characterizations (Table 3) were uniform throughout chromatograms, however, for spots with mixed color indications, it is possible that more than one phenolic compound is present. Spot numbers 11 and 15 (Fig. 6) were subdivided because color and close proximity of spots prevented contrasting delineations.

Summary phenolic patterns (Table 4) for each taxon were compiled using the total number of spots found in each taxon. Infrageneric and intergeneric comparisons of summary phenolic patterns were based on positive matches (a spot occurring in two taxa compared) and differences (a spot occurring in one of the taxa compared but not in the other). The degree of relationship between pairs of taxa was calculated using the coefficient of similarity $\frac{p}{p+d}$, where p represents the positive matches and d the differences. Coefficients vary from 0 (no resemblance) to 1 (identity).

Chromatographic patterns were subject to interpretation, although delimitations of infraspecific and interspecific taxa of *Pontederia* were not based strictly on phenolic patterns. Chromatograms were initially separated as to summary phenolic patterns (Table 4) in accordance with the morphological concept of taxa (see Taxonomy section). This morphological alignment of taxa was reinforced by the high coefficients of similarity (Fig. 7) obtained among taxa. The nine spots shared in common by all taxa of *Pontederia* examined (Table 4) are perhaps chemical

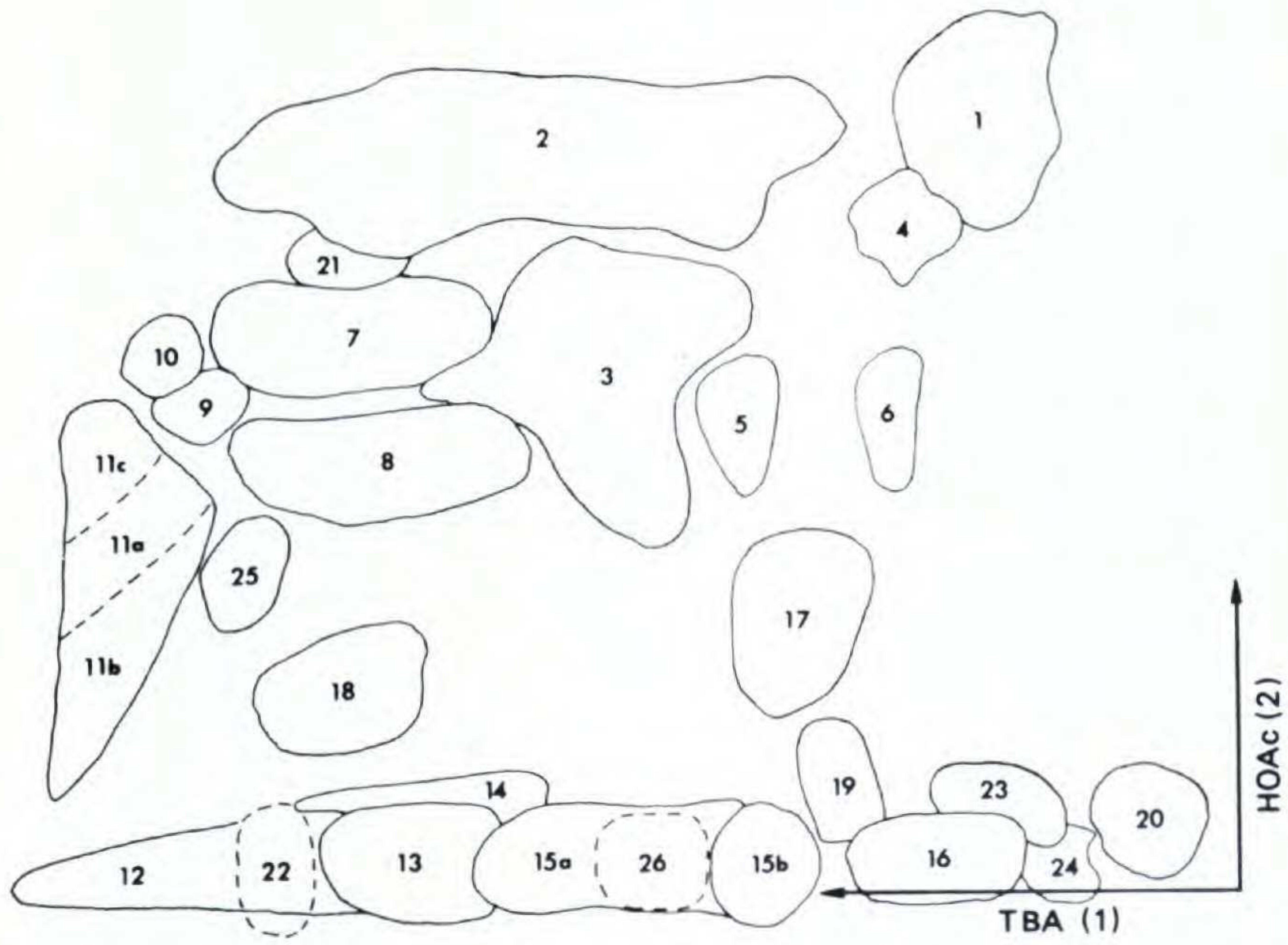

Figure 6. Summary two-dimensional paper chromatographic profile of phenolic compounds found in *Pontederia* and related genera.

indications of a similar operative genetics clearly visible by the close morphological identity among principal taxa.

Infrageneric comparisons (Fig. 7) indicate higher identity among typical *Pontederia cordata, P. sagittata, P. parviflora* and *P. rotundifolia* than among these taxa with *P. cordata* varieties *lancifolia* and *ovalis*. There was a stronger affinity of these two varieties with *P. rotundifolia* and *P. parviflora* than with typical *P. cordata*. This affinity should be tested further considering the very small sample sizes of varieties *lancifolia* and *ovalis* (Table 4).

High phenolic identity, greater variation in phenolic patterns, greater morphological similarity and like chromosome complement were found between typical *P. cordata* and *P. sagittata,* each containing an isolated spot (spot 15b and 22 respectively). Perhaps these single isolated spots are the development of metabolic pathways in fairly restricted geographical regions (Figs. 10-12, 15-16). The highest phenolic similarity was between *P. parviflora* and *P. rotundifolia*. Partial and fluctuating geographical isolation in Central and South America (Figs. 19, 22, 25)

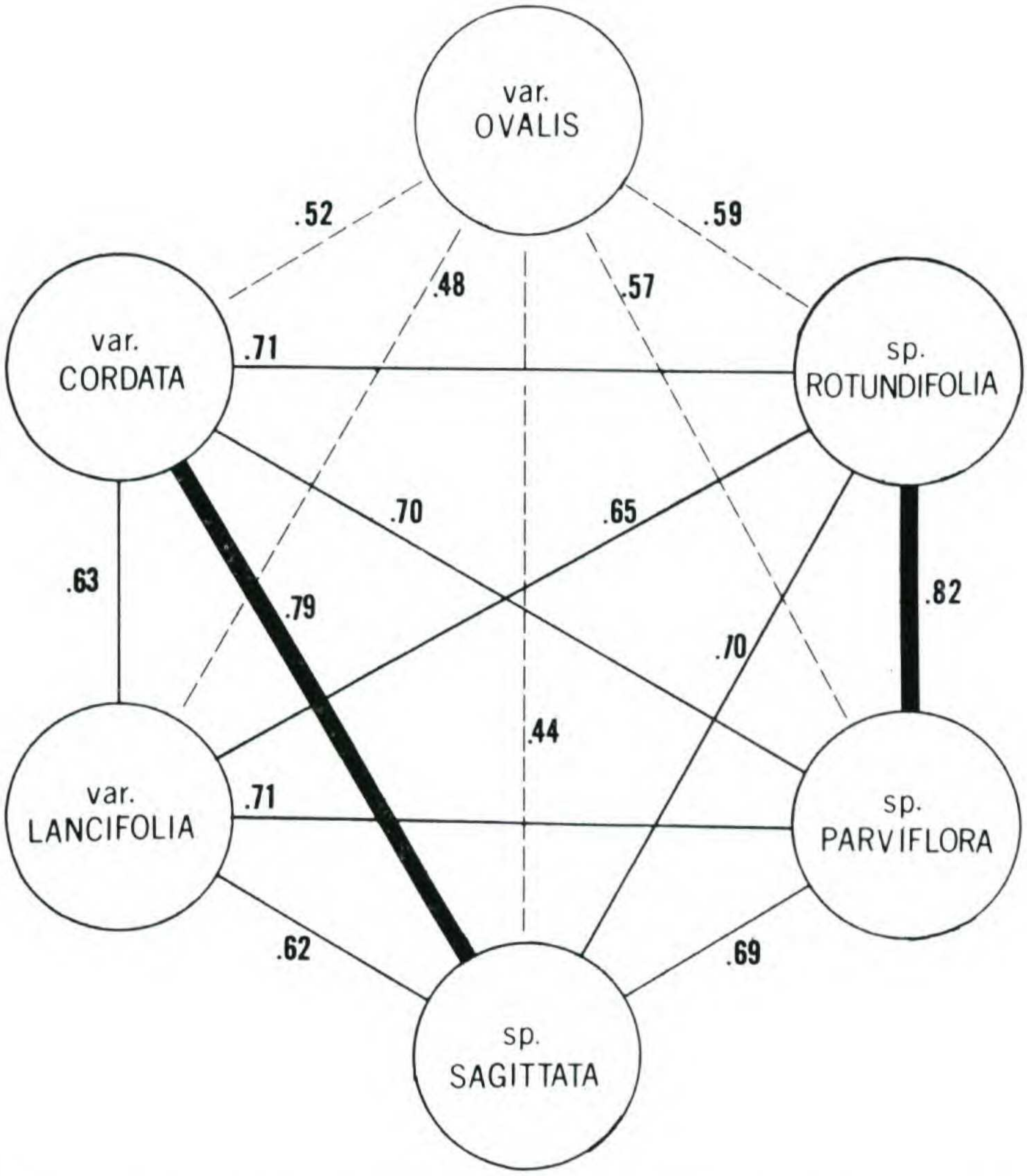

Figure 7. Graphic representation comparing two dimensional paper chromatographic profiles of *Pontederia* based on coefficients of similarity.

could account for a parallel and independent development or loss of metabolic systems in these two morphologically and cytologically distinct species.

Intergeneric comparisons of phenolic patterns and morphology reveal a greater difference between *Pontederia, Eichhornia* and *Heteranthera* than among taxa of *Pontederia.* Seven out of the nine spots common to *Pontederia* taxa were shared equally with *Eichhornia* and *Heteranthera* taxa examined. No spots (Table 4) were added to the total number of spots found in *Pontederia* by the inclusion of *Eichhornia* and *Heteranthera* taxa. Undoubtedly similar metabolic systems have evolved in the Neotropical Pontederiaceae, perhaps divergently from an ancestral system comparable with that found in typical *P. cordata* and *P. sagittata.*

EVOLUTIONARY CONSIDERATIONS

A speculative origin of *Pontederia* is attempted based on the present studies. The ancestral stock is hypothesized as aquatic, tropical in origin, inflorescence a many-flowered spike, fruit a one-seeded utricle, ovule pendulous, tristylous, six stamens, flowers zygomorphic and perianth parts basally connate. Cytological evidence indicates a haploid base chromosome number of $x=8$. Chromatographic patterns of phenolic compounds suggest that similar metabolic systems have evolved.

By the Lower Eocene, *Pontederia* had a restricted tropical range from South America to North America via the Middle American landbridge. On several occasions from the Upper Eocene to the Lower Pliocene (Schuchert, 1935) portions of Middle America were inundated. Speciation occurred in isolated areas as this isthmian landbridge rose and fell. Changes in environmental conditions (Baker, 1970), due in part to climatic instability and mountain building, were accompanied by floristic changes. A component of this change was *Pontederia* which persists today throughout Middle America.

Pontederia spread from Middle America into North

America where it had perhaps at one time a more western distribution as indicated by the Green River Formation of Eocene Age. *Pontederites* (Knowlton, 1922) was described from the lake margin fossil flora of the Green River Formation in northwestern Colorado and the Gosiute Lake in southwestern Wyoming. The fossil material is an upper portion of a leaf fragment which looks like the characteristic venation of living *Pontederia.* The Green River Formation was bordered on the north and west by the Rocky Mountains. The barriers were less containing to the east and south towards the Gulf Coastal Plain which was covered with water during the Eocene. As the water receded *Pontederia* was redistributed to the warmer subtropical climate of the Gulf Coastal Plain where it started to inhabit the Atlantic Coastal Plain of North America. The Appalachian Mountains (Core, 1966) were then and still are the main obstacle (Fig. 11) to its spread into the interior of the eastern United States.

The advent of the Pleistocene brought deleterious climatic changes resulting in a restricted southerly distribution of *Pontederia* toward the warmer climate of the Gulf Coast. As the climate fluctuated during glacial and interglacial periods, fluctuations also occurred in the distribution of *Pontederia* along the Atlantic Coast. Glacial withdrawal (Sculthorpe, 1967) brought an increasing warmth accompanied by an optimum post glacial maximum warmth, culminating in today's climatic conditions. The retreat of the last ice-sheets left behind numerous lakes, bogs and ponds. Since the Wisconsin glacier, *Pontederia* has spread and thrived throughout these aquatic glacial remnants of eastern North America reaching its present northern and northwestern limits within relatively recent times.

TAXONOMY OF PONTEDERIA L.

Pontederia L., Sp. Pl. 288. 1753. Gen. Pl. ed. 5, 140. 1754. Lectotype: *Pontederia cordata* L.

Umsema Raf. [*Unisema* Raf., Med. Fl. 2: 105. 1830.], Med. Repos. II 5: 352. 1808.

Reussia Endl., Gen. Pl. 1: 139. 1836. Type: *Reussia triflora* Endl. ex Seub. = *Pontederia subovata* (Seub.) Lowden.

Perennial emersed herbs. Rhizomes branched, aerial stems erect or prostrate. Leaves obtuse; margins entire with parallel outwardly curved venation; blades (phyllodes) lanceolate, ovate, cordate, sagittate, hastate or reniform; foliage dark green to grayish, often containing anthocyanin. Petiole of floral shoot leaf short; petioles of other leaves long; bases sheathed and clasping, sheaths ligulate. Inflorescence a few to many flowered spike enclosed (early in floral development) by a spathe (the most terminal phyllode of the floral shoot) and petiole base of the flower stalk leaf; peduncles longest with maturation of infructescences and subtended by the spathe; sheath (expanded phyllode base) in axil of floral shoot. Flowers bisporangiate, zygomorphic (bilaterally symmetrical), bilabiate, blue to purple, white or white-green, largest perianth lobe with a bilobed yellow spot; perigone (perianth) of 6 basally connate parts; stamens 6 unequal, in two groups of 3 each, adnate to the perigone tube; anthers introrse, dorsifixed, versatile, dehiscing longitudinally; filaments and perigone tube covered with hairs terminated in pinheadlike glands; stigmas 3-lobed, each lobe bifid; tristylous or homostylous species; carpels originally 3, united, 2 aborted and 1 fertile, unilocular, 1-seeded; ovules pendulous, anatropous, placentation parietal. Fruit a utricle, 1-seeded, indehiscent; enclosed by a hardened perigone base, toothed, smooth or spinulose ridged; pericarp high in glutanous content. Seeds reniform or ovoid; endosperm white, copious, surrounding a cylindrical embryo.

Key To The Taxa

a. Hardened perigones toothed or smooth ridged (Fig. 1A-C); floral bearing shoots erect (subgenus *Pontederia*). . . . . *b.*

b. Style length unequal to stamen length (Fig. 3A-C) . . . . *c.*

c. Hardened perigones toothed ridged (Fig. 1A) .... *d.*

d. Leaves cordate, sagittate (unauricled), hastate or reniform .... 1a. *P. cordata* var. *cordata*

d. Leaves narrow to broadly lanceolate (leaf base not lobed) .... 1b. *P. cordata* var. *lancifolia*

d. Leaves ovate to ovate-lanceolate (leaf base not lobed); peduncles hairy .... 1c. *P. cordata* var. *ovalis*

c. Hardened perigones smooth ridged (Fig. 1B); leaves sagittate (usually deeply auricled) .... 2. *P. sagittata*

b. Style as long as the three longest stamens (Fig. 3D); leaves subcordate .... 3. *P. parviflora*

a. Hardened perigones spinulose ridged (Fig. 1D); floral bearing shoots prostrate (subgenus *Reussia*) ...... *e.*

e. Flowers long lasting (more than 8 flowers per inflorescence); leaves reniform, sagittate or cordate .... 4. *P. rotundifolia*

e. Flowers ephemeral (usually fewer than 12 flowers per inflorescence); leaves subovate, sublanceolate or elliptical .... 5. *P. subovata*

I. *Pontederia* subg. *Pontederia* (Lectotype: *Pontederia cordata* L.)

Hardened perigone bases toothed or smooth ridged (Fig. 1A-C); floral bearing shoots erect; aerial stems with short internodes; underground rhizomes long (mature plants).

Subgenus *Pontederia* is found 50° North to 35° South of the equator in the Americas.

1. *Pontederia cordata* L., Sp. Pl. 288. 1753.

Plants 9-13 dm tall. Leaves cordate, sagittate (unauricled), ovate or lanceolate; blades 0.4-21 cm wide; spathe (terminal phyllode of floral shoot) 2-7.4 cm long; petiole of floral shoot leaf (includes sheath base) 4-31 cm long; petiole of other leaves 28.7-59.5 cm long, ligule of petiole sheath 4-10.5 cm long; sheath in axil of floral shoots 22.3-

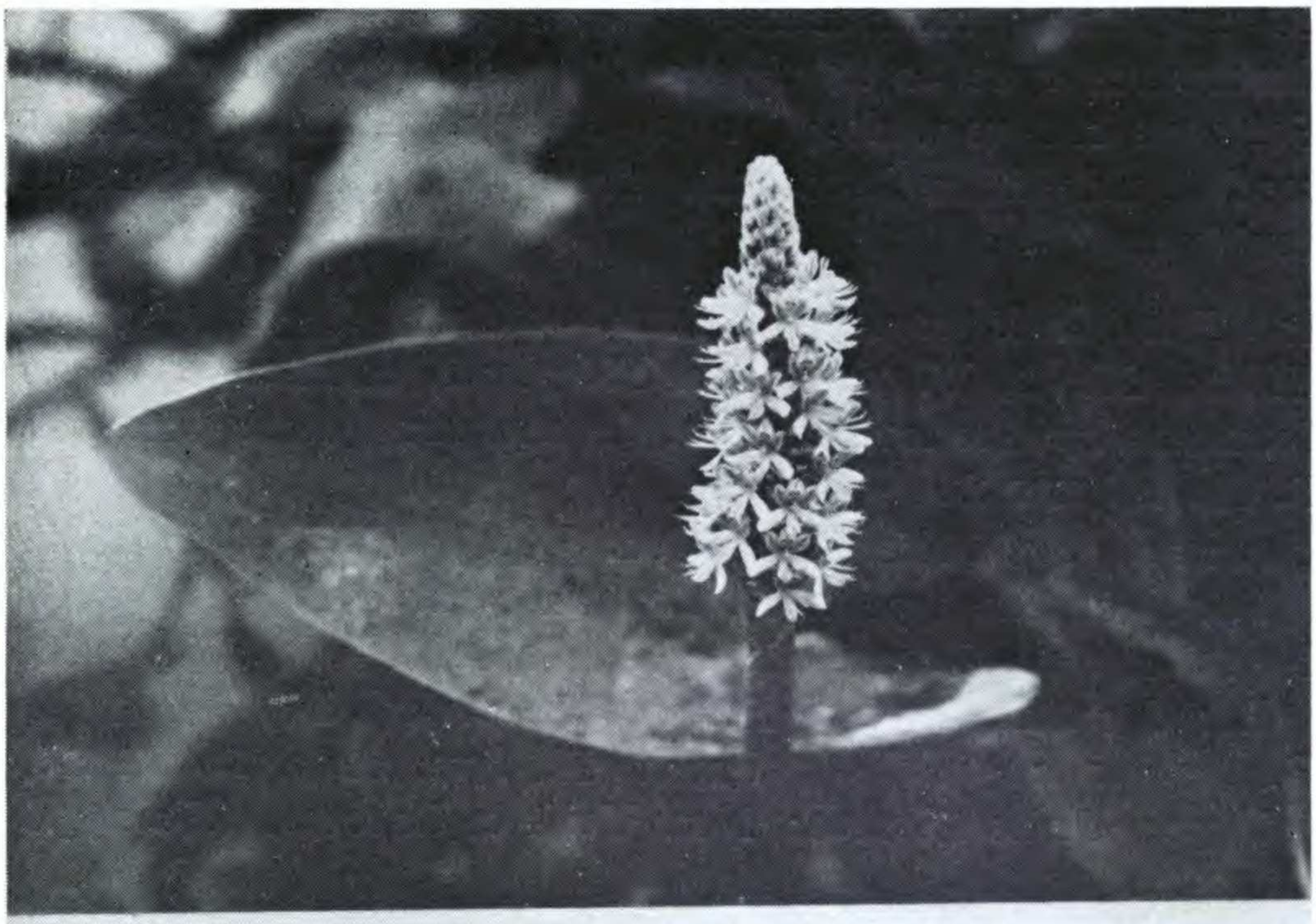

Figure 8. Inflorescence, clasping subtending spathe and flowering stalk leaf of *Pontederia cordata* var. *cordata,* U.S., Ohio, Ottawa County (*Lowden* photo, Jul 1966); upper figure.

Figure 9. Clones of *Pontederia cordata* var. *cordata* in marsh habitat, U.S., Ohio, Ottawa County (*Lowden* photo, Jul 1966); lower figure.

28 cm long. Inflorescence 2-16 cm long; peduncle (inflorescence base to floral shoot leaf base) 5-33 cm long. Perigone blue to white; hardened perigone bases (Fig. 1A) toothed ridged; anthers blue. Tristylous. Fruits and seeds reniform.

1a. *Pontederia cordata* L. var. *cordata*. Type missing: United States, Virginia and Maryland, communicated to Linnaeus by Gronovius. Neotype chosen: [Savage, 407.4] *P. Kalm* (LINN).

Umsema obtusifolia Raf., Med. Repos. II, 5: 352. 1808. Based on the type of *Pontederia cordata* L.

Umsema mucronata Raf., Med. Repos. II, 5: 352. 1808. Based on the type of *Pontederia cordata* L.

Pontederia angustifolia Pursh, Fl. Am. Sept. 224. 1814. Type: United States: New York to Carolina (Holotype OXF?).

?*Unisema sagitata* Raf., Fl. Ludov. 18. 1817. Type not seen.

Pontederia cordata L. var. *angustifolia* (Pursh) Torrey, Fl. U.S. 1: 343. 1824.

Unisema deltifolia Raf., Med. Fl. 2: 105, 107. 1830. Based on the type of *Pontederia cordata* L.

Unisema purshiana Raf., Med. Fl. 2: 107. 1830. Based on the type of *Pontederia angustifolia* Pursh.

Unisema media Raf., Med. Fl. 2: 107. 1830. Type: United States: "New York to Carolina" (Holotype NY!).

Unisema media Raf. var. *albiflora* Raf., Med. Fl. 2: 107. 1830. Type not seen.

Unisema media Raf. var. *angustifolia* Raf., Med. Fl. 2: 107. 1830. Type not seen.

Unisema obliquata Raf., Med. Fl. 2: 107. 1830. Type: United States: "New Jersey and Virginia". Type not seen.

Unisema latifolia Raf., Med. Fl. 2: 107. 1830. Type: United States: "Southern States". Type not seen.

Unisema latifolia Raf. var. *elatior* Raf., Med. Fl. 2: 107. 1830. Type not seen.

Unisema latifolia Raf. var. *undulata* Raf., Med. Fl. 2: 107. 1830. Type not seen.

Unisema latifolia Raf. var. *albiflora* Raf., Med. Fl. 2: 107. 1830. Type not seen.

Unisema latifolia Raf. var. *pallida* Raf., Med. Fl. 2: 107. 1830. Type not seen.

Unisema acutifolia Raf., Med. Fl. 2: 107. 1830. Type: United States: Carolina. Type not seen.

Unisema heterophylla Raf., Med. Fl. 2: 108. 1830. Type: United States: "New York to Louisiana". Type not seen.

Unisema heterophylla Raf. var. *lanceolata* Raf., Med. Fl. 2: 108. 1830. Type not seen.

Unisema heterophylla Raf. var. *stenocardia* Raf., Med. Fl. 2: 108. 1830. Type not seen.

Unisema rotundifolia Raf., Med. Fl. 2: 108. 1830. Type: United States: "Western States" [Rafinesque (1837); "Kentucky and Illinois"]. Type not seen.

Pontederia cordata L. var. *albiflora* Short, Transylvania J. Med. Assoc. Sci. 32: 3, 7. 1835. Type: United States: Kentucky, marshes around Louisville, *C. W. Short* (Holotype PH!; isotype NY!).

Pontederia caerulea Maund, Bot. Gard. 6: 551. 1836. Type: Great Britain, plant under cultivation, introduced 1830. Type not seen.

Unisema peduncularis Raf., New Fl. 2: 75. 1837. Based on the type of *Pontederia angustifolia* Pursh.

Unisema peduncularis Raf. var. *parvifolia* Raf., New Fl. 2: 75. 1837. Type not seen.

Pontederia nymphaeifolia Kunth, Enum. Pl. 4: 126. 1843. Type: Brazil: *Sello* 235 (Holotype B?, photograph of holotype NY!; isotype PH!).

Pontederia cordata L. var. *typica*, Solms in DC. Monog. Phan. 4: 532, in part. 1883. [that part based on the types of *Pontederia cordata* L., *P. angustifolia* Pursh and *P. cordata* L. forma *brasiliensis* Solms in DC.]

Pontederia cordata L. forma *angustifolia* (Pursh) Solms in DC., Monog. Phan. 4: 532, in part. 1883. [that part based on the type of *Pontederia angustifolia* Pursh]

Pontederia cordata L. forma *brasiliensis* Solms in DC., Monog. Phan. 4: 533. 1883. Type not seen.

Pontederia rotundifolia L. f. var. *nymphaeifolia* (Kunth) Solms in DC. Monog. Phan. 4: 534. 1883.

Pontederia cordata L. [var.] *lancifolia* (Muhl.) Morong. Mem. Torrey Bot. Club 5: 105, in part. 1894. [that part based on types of *Pontederia cordata* L. and *P. angustifolia* Pursh]

Narukila cordata (L.) Nieuwland, Amer. Midl. Naturalist 3: 101. 1913.

Narukila cordata (L.) Nieuwland var. *lancifolia* (Muhl.) Nieuwland, Amer. Midl. Naturalist 3: 101, in part. 1913. [that part based on the types of *Pontederia cordata* L. and *P. angustifolia* Pursh]

Pontederia cordata L. forma *angustifolia* (Pursh) House, New York State Mus. Bull. 243-244: 62. 1923.

Pontederia cordata L. forma *latifolia* (Raf.) House, New York State Mus. Bull. 243-244: 62. 1923.

Pontederia cordata L. forma *albiflora* (Raf.) House, New York State Mus. Bull. 243-244: 62. 1923. Based on the type of *Unisema media* Raf. var. *albiflora* Raf.

Unisema cordata (L.) Farwell, Pap. Michigan Acad. Sci. 3: 91. 1924.

Unisema cordata (L.) Farwell forma *angustifolia* (Pursh) Farwell, Pap. Michigan Acad. Sci. 3: 92. 1924.

Unisema cordata (L.) Farwell forma *latifolia* Farwell, Pap. Michigan Acad. Sci. 3: 92. 1924. Type: United States: New Jersey: Secancus, 15 Sept. 1890, *H. H. Rusby* (Lectotype MICH!); Franklin, Aug. 1873, *H. H. Rusby* (Syntype MICH!).

Pontederia lanceolata Nutt. forma *trullifolia* Fernald, Rhodora 27: 81. 1925. Type: United States: Florida, Okeechobee region, Brevard Co., 3 August 1903, *A. Fredholm* 5927 (Holotype GH!).

Pontederia lanceolata Nutt. forma *brasiliensis* (Solms) Fernald, Rhodora 27: 81. 1925.

Unisema lancifolia (Muhl.) Farwell forma *trullifolia* (Fernald) Farwell, Amer. Midl. Naturalist 11: 73. 1928.

Pontederia cordata L. forma *taenia* Fassett, Rhodora **39:** 274. 1937. Type: United States: Maine, Lincoln Co. Damariscotta Lake, Jefferson, shallow mucky cove, 28 August 1936, *N. C. Fassett* 16067 (Holotype WIS!; isotypes GH!, MO!).

Pontederia cordata L. forma *bernardi* Lepage, Naturaliste Canad. **82:** 101. 1955. Type: Canada: Quebec, Nominingue, zone tourbeuse autour du lac Violon, 12 aout 1951, *Jean-Paul Bernard* 386 (Holotype CAN!).

Plants up to 11 dm tall (Fig. 9). Leaves cordate (Fig. 8), rarely auricled, or sagittate (unauricled), blades 2.2-21 cm wide; spathe (terminal phyllode of floral shoot) 2-7.4 cm long; petiole of floral shoot leaf (includes sheath base) 4-31 cm long; petiole of other leaves 28.7-59.5 cm long, ligule of petiole sheath up to 10.5 cm long; sheath in axil of floral shoots up to 28 cm long. Inflorescence (Fig. 8) 2-16 cm long; peduncle (inflorescence base to floral shoot leaf base) 5-33 cm long. Perigone blue, purple or white.

In North America restricted to the eastern provinces of Canada (Fig. 10; Ontario, Quebec, New Brunswick, Prince Edward Island and Nova Scotia) and the eastern to midwestern United States (Fig. 11) with greatest concentration along the Atlantic Coastal Plain and the Great Lakes Region as compared with the Mississippi embayment. In Middle America known only from British Honduras (Fig. 12). In South America (Fig. 15) found in Argentina, Brazil, Colombia, Paraguay and Uruguay.

Representative Specimens: CANADA. **Province New Brunswick.** Norton, 20 Aug 1876, *Hay* (CAN). **Province Nova Scotia.** COLCHESTER CO.: Earltown Lake, 29 Jul 1954, *Smith, Webster & Bentley* 11742 (CAN). CAPE BRETON ISLAND: Louisburg, 19 Aug 1898, *Macoun* (CAN). **Province Ontario.** Vermilion River between Lake Superior and Lake Nipissing near Whitefish, 13 Aug 1936, *Grassl* 7494 (MICH). PELEE ISLAND: Essex Co., lagoon N end, 17 Aug 1967, *Stuckey* 5161 (OS). GEORGIAN BAY AREA: Go Home, O.G.U. (CAN). **Province Quebec.** Bell's Lake near Wakefield, 24 Jul 1903, *Macoun* (CAN). UNITED STATES. **Alabama.** BALDWIN CO.: Battleship Parkway, 4 mi E of Mobile, Routes 31-90-38, Mobile Bay Causeway, 15 Jul 1970, *Lowden* 5 (OS). **Arkansas.** CRAIGHEAD CO.: Lake City, *Demaree* 7075 (US).

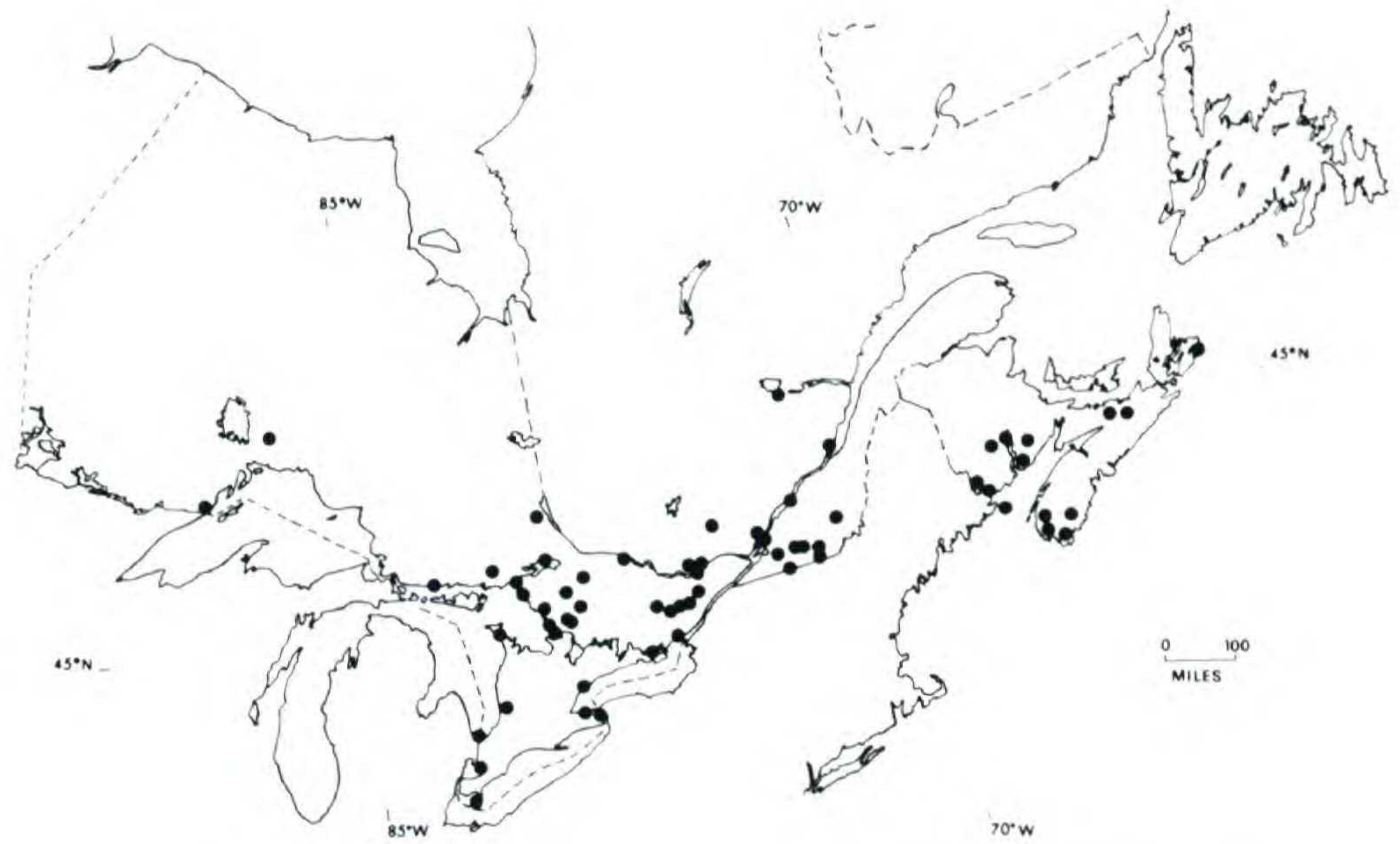

Figure 10. Distribution of *Pontederia cordata* var. *cordata* in Ontario, Quebec, New Brunswick, Prince Edward Island and Nova Scotia Provinces of Canada.

Connecticut. FAIRFIELD CO.: Green Pond, Sherman, 4 Sep 1916, *Pennell* 8592 (PH). **Delaware.** NEW CASTLE CO.: Wilmington, 6 Jul 1843, *Brakely* (PH). **District of Columbia.** Potomac bank, Washington, 28 Jun 1891, *Blanchard* (MO-2). **Florida.** ALACHUA CO.: 2 mi S of Gainesville, 17 May 1940, *Martin* 1457 (DUKE). **Georgia.** LONG CO.: Altamaha River Swamp, 4½ mi SW of Ludowici, 10 Jun 1950, *Duncan* 11089 (GH). **Illinois.** COOK CO.: 131St between Wolf Rd and Will-Cook Rd W of Palos Park Pond, 16 Aug 1941, *Steyermark* 40917 (F). **Indiana.** DEKALB CO.: Diamond Lake, 35 mi N of Auburn, 30 Jul 1933, *Shoop* (F). **Iowa.** BENTON CO.: Vinton, 1879, *Davis* (WIS). **Kentucky.** BALLARD CO.: Wickliffe, Swan Pond, 18 Aug 1923, *McFarland & Anderson* 167 (MO). **Louisiana.** BEAUREGARD PARISH: Near Longville, 29 Apr 1955, *Cooley & Brass* 4072 (GH). **Maine.** LINCOLN CO.: 3 mi S of Newcastle Center off Route 1, 3 Sep 1969, *Lowden* 31 (OS). SAGADAHOC CO.: Cathance River, 1 mi from Topsham, 1½ mi from Bowdoinham, 3 Sep 1969, *Lowden* 29 (OS); Foreside Road near Topsham off Route 24, 3 Sep 1969, *Lowden* 30 (OS). YORK CO.: Bonnie Bay Pond, North Berwick, W of Route 4, 2 Jul 1970, *Lowden* 1 (OS); Kennebunk River, boundary between Kennebunk and Arundel, Route 95, Jul 1970, *Lowden* 4 (OS). **Maryland.** CECIL CO.: Chesapeake City, 7-11 1923, *Tidestrom* 11402 (GH). **Massachusetts.** BARNSTABLE CO.: Hyannisport, 22 Aug 1888, *Churchill* (MO). **Michigan.** BARRY CO.: Long Lake, 14 Aug 1936, *Woodbury* 317 (MICH). **Minne-**

Figure 11. Distribution of *Pontederia cordata* var. *cordata* (dots) and var. *lancifolia* (triangles) in the United States.

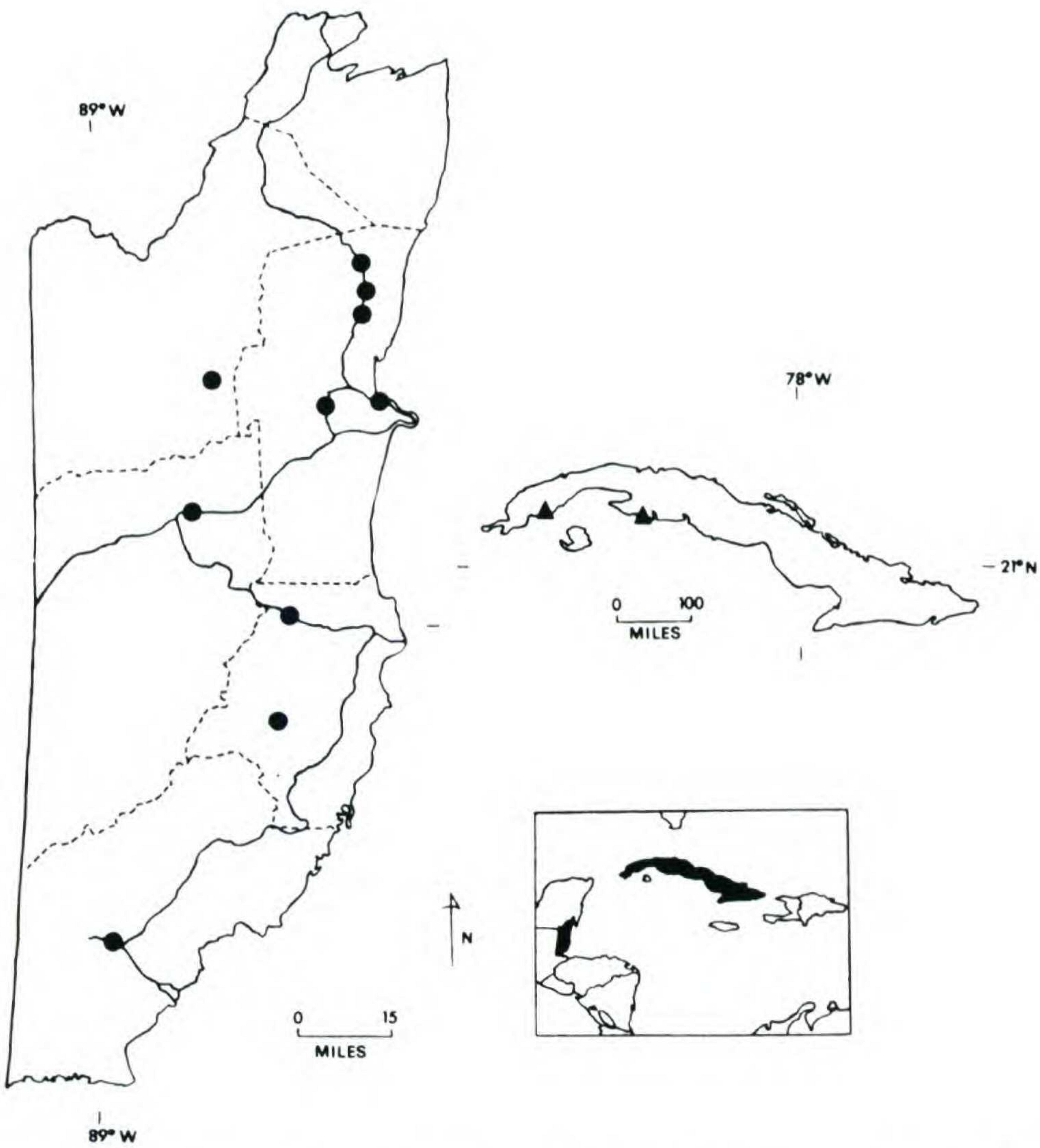

Figure 12. Distribution of *Pontederia cordata* var. *cordata* (dots) in British Honduras (solid lines represent highways), C.A., and var. *lancifolia* (triangles) in Cuba, West Indies.

sota. AITKEN CO.: Rice Lake, Aug 1921, *Kubichek* 143 (MO). **Mississippi.** HANCOCK CO.: Jordan River S of Kiln, 29 Apr 1967, *Jones* 11846 (FSU). **Missouri.** BATES CO.: Prairie Lake, Cygnes River, 1¼ mi SW of Rapinsville, 1 Oct 1938, *Steyermark* 9975 (F, MO). **New Hampshire.** ROCKINGHAM CO.: Exeter River, Philips Exeter Academy, Exeter, 8 Sep 1969, *Lowden* 32 (OS). STRAFFORD CO.: Bellamy River, Exit 7 Spaulding Turnpike, 4 Jul 1970, *Lowden* 2 (OS). **New Jersey.** ATLANTIC CO.: Pleasant Mills, 4 Aug 1907, *Bartram* (PH). **New York.** ESSEX CO.: Lake Harris, Newcomb, 1 Aug 1921, *House* 8431 (CAN). **North Carolina.** BEAUFORT CO.: Cockold Creek, near Bellhaven, 25 Jun 1935, *Correll* 1703 (DUKE). **Ohio.** DEFIANCE CO.: Little Pond off Route 49, 22 Sep 1969, *Lowden* 34 (OS); Big Pond off Route 49, 22 Sep 1969, *Lowden* 35 (OS). LICKING CO.: Cranberry Bog, Buckeye Lake, 12 Oct 1969, *Lowden* 33 (OS). OTTAWA CO.: Winous Pt., 3½ mi SW of Port Clinton off Route 53, 10 Aug 1969, *Lowden* 36 (OS); Winous Pt., 27 Jun 1969, *Lowden* 37 (OS). **Oklahoma.** CHEROKEE CO.: Tahlequah, 21 Jun 1936, *Gruchy* 135 (GH, NY). **Pennsylvania.** BUCKS CO.: Neshaminy Creek, Bridge Point [Edison], 22 Jul 1876, *Meredith* (PH). **Rhode Island.** NEWPORT CO.: Tiverton, Sawdy Pond, 16 Jul 1932, *Sanford* (NEBC). **South Carolina.** ANDERSON CO.: Piedmont, 17 Jul 1919, *Davis* (BKL, MO). **Tennessee.** GRUNDY CO.: Goose Pond, near Pelham, 27 Apr 1936, *Svenson* 7610 (BKL). **Texas.** BEXAR CO.: San Antonio, 3 Oct 1900, *Bush* 1258 (MO). **Vermont.** ESSEX CO.: Bow Pond, Guildhall, 30 Aug 1940, *Pease* 28364 (NEBC). **Virginia.** FAIRFAX CO.: Near Great Falls, 7 Aug 1910, *Dowell* 6435 (GH). **Wisconsin.** ASHLAND CO.: Torrey L., Morse, 16 Jul 1936, *Knowlton* 97 (WIS). CENTRAL AMERICA. **British Honduras.** BELIZE DISTRICT: Northern River, Nov 1933, *Gentle* 944 (GH, MICH, MO, NY); 9 mi N of Belize City, Northern Highway, 24 Dec 1969, *Lowden* 24 (OS); 29 mi N of Belize City, Cowhead Creek, Northern Highway, 30 Dec 1969, *Lowden* 26 (OS); 32 mi N of Belize City, Northern Highway, 30 Dec 1969, *Lowden* 27 (OS); Hattieville-Burrell Boom Road, 5½ mi from Burrell Boom, 30 Dec 1969, *Lowden* 28 (OS). COROZAL DISTRICT: 1931-1932, *Gentle* 388 (F, MICH, US). EL CAYO DISTRICT: 41 mi Sect., Belize-Cayo Road, 1 Apr 1958, *Gentle* 9708 (DUKE, F, MICH, NY, US). ORANGE WALK DISTRICT: Hillbank Lagoon, Feb 1933, *Pelly* 43, 44 (F). STANN CREEK DISTRICT: Cockscomb vic., 18 Jun [1930], *Schipp* S119 (F); 23 mi, Stann Creek Valley, 11 Mar 1932, *Schipp* 955 (F, GH, MICH, MO, NY). TOLEDO DISTRICT: 15 mi, San Antonio-Punta Gorda Road, 28 Nov 1951, *Gentle* 7531 (F, NY, US). SOUTH AMERICA. **Argentina.** PROVINCIA BUENAS AIRES: Depto. Campana, Campana, 27 Nov 1938, *Eyerdam & Beetle* 23070 (GH). PROVINCIA CHACO: Dept. Resistencia, Colonia Benitez, 12 Dec 1928, *Venturi* 7907 (GH, US). PROVINCIA CORRIENTES: Mercedes, 12 leguas al N, XI 1936, *Rodrigo* 750 (NY). PROVINCIA MISIONES: Dept. Apostoles, Tres Galpones, 8 II 1947, *Huidobro* 4817 (MO). TERRITORY FORMOSA: Formosa, 5-1918, *Jorgensen* 3005 (MO). **Brazil.** PARANA: Rio Pequeno, auto estude Curitiba-Paranagua, XI 1960, *Brage* & *Vesreira* 320 (US). PROV. MINAS GERAIS: Brasilia (PH). RIO DE JANEIRO: Brasilia, pr. Lorena, *L. Riedel*, iter Brasiliensis 1821-36 (NY). RIO GRANDE DO SUL: Logoa dos Barros, pr. Osorio, 24 Nov 1949, *Rambo* 44574 (F). SANTA CATARINA: Mun. Chapeco, Fazenda Campo Sao Vicente, 24 km W of Campo Ere, *Smith, Reitz* & *Sufridini* 9468, 9482 (US). SAO PAULO: Butantan, 17 Oct 1917, *Hoehne* 726 (NY). **Colombia.** COMMISSARIA MAGALENA: Near Valencia, 12 Oct 1944, *Haught* 4406 (F, US). COMMISSARIA VALLE [DEL CAUCA]: Costa del Pacifico, rio Cajambre, Quebrada de Guapecito, 16 May 1944, *Cuatrecasas* 17703 (F). **Paraguay.** Paraguaria Centralis, lacus Ypacaray, Nov 1913, *Hassler* 12683 (GH, MO, NY, US); Dep. Paraguari, Paraguari, Cerro Hu, 25 Nov 1950, *Vervoorst* 564 (MO). **Uruguay.** DEPARTMENT CANELONES: Loc. Dict. Toledo, Nov 1926, *Herter* 522 (F, GH, MO, NY, WIS). DEPARTMENT MALDONADO: Lau [San] Carlos, M 1 1941 *Descole* 104 (GH).

Since none of the original material was located the specimen of Kalm in the Linnaean Herbarium by 1751 was selected as neotype. The numerous names of Rafinesque are placed in synonomy based on their leaf descriptions and geographical locations. A complete list of specimens examined is included in my original dissertation.

The specimens from British Honduras are of particular interest in considering the puzzling disjunct distributions of both *Pontederia cordata* varieties *cordata* and *lancifolia* in North and South America. Actually these specimens are somewhat intermediate between typical *P. cordata* and *P. sagittata*. They have tooth ridged hardened perigone bases like *P. cordata* (Fig. 1A) with the overall perigone shape of *P. sagittata* (Fig. 1B). The leaves have deep sinuses giving the appearance of being slightly auricled. A hybrid origin is suggestive; however, an overlap in geographical ranges between *P. cordata* var. *cordata* and *P. sagittata* is not evident. The specimens in general are more characteristic of *P. cordata* var. *cordata*.

1b. *Pontederia cordata* L. var. *lancifolia* (Muhl.) Torrey, Fl. U.S. **1**: 343. 1824.

Pontederia lancifolia Muhl., Cat. 34. 1813. Type: United States: Car. [Carolina] (Lectotype chosen, PH!), Figure 13.

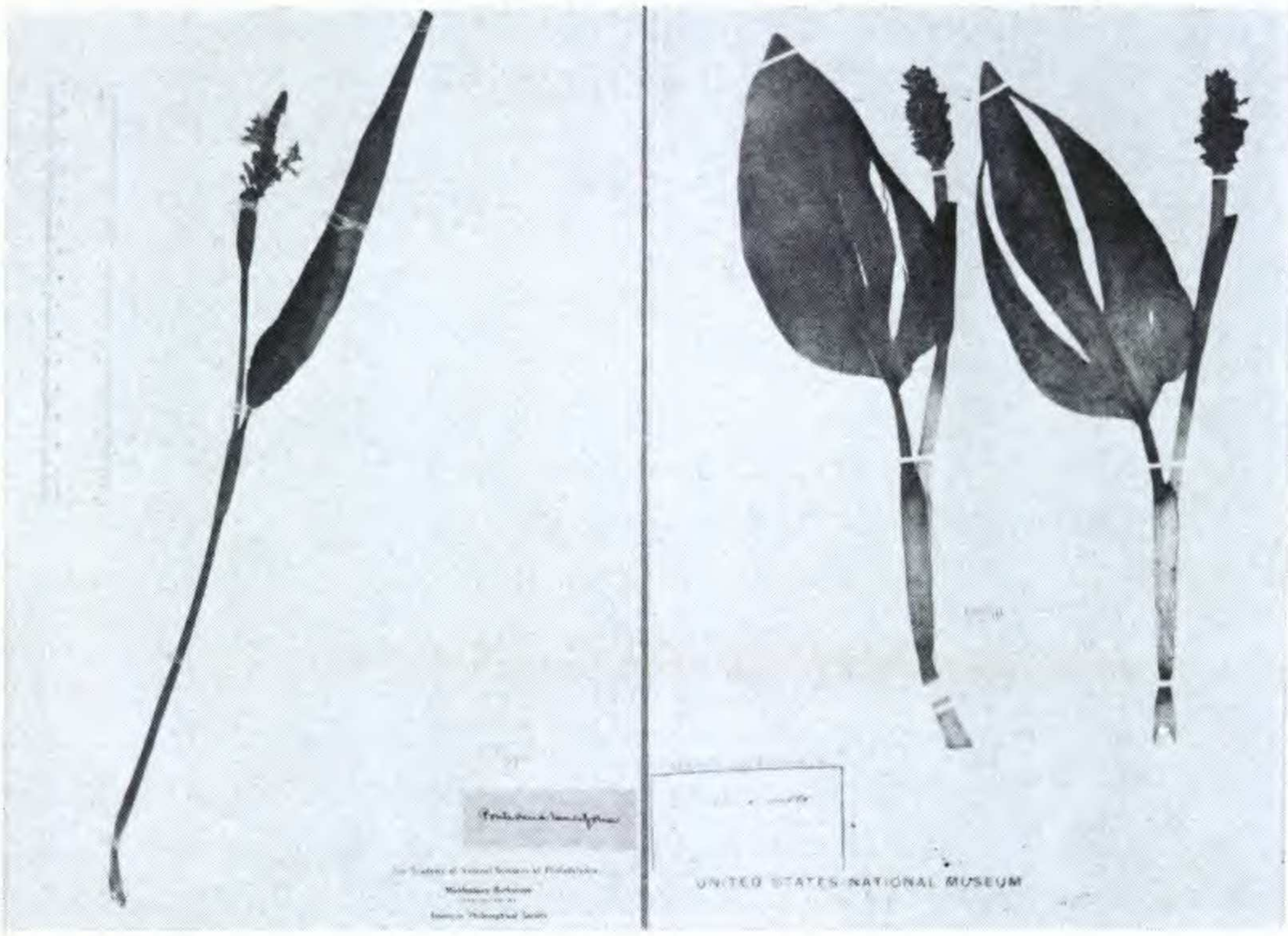

Figure 13. *Pontederia cordata* var. *lancifolia*. Lectotype of *P. lancifolia* Muhl. in the Muhlenberg Herbarium (PH), showing a narrow lanceolate flowering stalk leaf; at left.

Figure 14. *Pontederia cordata* var. *ovalis*. Holotype of *P. ovalis* Mart. in Roemer & Schultes, showing ovate leaves and hairy peduncles; at right.

Pontederia lanceolata Nuttall, Gen. **1**: 216. 1818. Type: United States: Savannah, Georgia [*W. Baldwyn*] (Holotype PH!).

Unisema lancifolia Raf., Alt. Jour. 178. 1833. Based on the type of *Pontederia lancifolia* Muhl.

Pontederia cordata L. var. *lanceolata* (Nutt.) Grisebach, Cat. Pl. Cub. 252. 1866.

Pontederia cordata L. var. *typica*, Solms in DC. Monog. Phan. **4**: 532, in part. 1883. [that part based on the type of *Pontederia lanceolata* Nutt.]

Pontederia cordata L. forma *angustifolia* (Pursh) Solms in DC. Monog. Phan. **4**: 533, in part. 1883. [that part based on the type of *Pontederia lanceolata* Nutt.]

Pontederia cordata L. *lancifolia* (Muhl.) Morong. Mem. Torrey Bot. Club **5**: 105, in part. 1894. [that part based on the type of *Pontederia lancifolia* Muhl.]

Narukila cordata (L.) Nieuwland var. *lancifolia* (Muhl.) Nieuwland, Amer. Midl. Naturalist **3**: 101, in part. 1913. [that part based on the type of *Pontederia lancifolia* Muhl.]

Pontederia heterantherimorpha (K. Schum. ex Schwartz) Schwartz in Engler, Bot. Jahrb. **61** (no. 139): 41. 1927. Type: Brazil: "Im Staate Goyaz, *A. Glaziou* 22228. Type not seen.

Unisema lancifolia (Muhl.) Farwell, Am. Midl. Nat. **11**: 73. 1928.

?*Pontederia oblonga* Larranaga, Pub. Inst. Hist. Geog. Uruguay **2**: 134. 1930. Type not seen.

Plants up to 13 dm tall. Leaves narrow lanceolate (Fig. 13) to broadly ovate-lanceolate, blades 0.4-8.3 cm wide; spathe (terminal phyllode of floral shoot) 2-6.5 cm long.; petiole of floral shoot leaf (includes sheath base) 4-21 cm long; petiole of other leaves 29-59.5 cm long, ligule of petiole sheath up to 10.5 cm long; sheath in axil of floral shoot up to 28 cm long. Inflorescence 2-15 cm long; peduncle (inflorescence base to floral shoot leaf base) 5-33 cm long. Perigone blue to blue purple.

In the United States (Fig. 11) concentrated along the

Gulf Coastal Plain of the southeast extending along the coasts of the northeastern Atlantic seaboard states. Along the southwestern coast of Cuba (Fig. 12), West Indies. In South America (Fig. 15) known from Argentina, Brazil, Colombia, Paraguay and Uruguay.

Representative Specimens. UNITED STATES. **Alabama.** GENEVA CO.: 8 mi S of Samson, 9 May 1967, *McDaniel* 8916 (FSU). **Connecticut.** NEW LONDON CO.: E Lyme, Dodge's Pond Niautic, 19 Aug 1913, *Harger* 6328 (NEBC). WINDHAM CO.: Thompson, Long Pond, 19 Aug 1918, *Weatherby* 4373 (NEBC). **District of Columbia.** Potomac River, Jun 1896, *Morris* 3046 (BKL). **Florida.** BAY CO.: Panama City, Mine Defense Lab vicinity, 1 May 1959, *Jones* (FSU). BREVARD CO.: Indian River near Rockledge, 10-20 Mar 1916, *Bartram* (PH). BROWARD CO.: 11 mi W of Davie, 31 Jan 1940, *Seibert* 1191 (MO, PH). COLLIER CO.: Pinecrest, S of Tamiami Trail between mi 40 and Ochopee, 15 Apr 1952, *Field & Lazar* (US). COLUMBIA CO.: 6 mi N of Lake City, 20 May 1964, *Godfrey* 63755 (FSU). DADE CO.: Everglades, W. of Miami, 1-9 Nov 1901, *Small & Nash* (NY). DE SOTA CO.: Arcadia, 14 Mar 1926, *Williams* (PH). DUVAL CO.: NE Forida, May, *Curtis* 2988 (BKL, F, GH, MO, NY, US). FRANKLIN CO.: 11 mi S of Sumatra, 24 Jul 1957, *Godfrey* 55715 (FSU, GH). GADSDEN CO.: 1 mi W of Ock[h]lockonee River, U.S. 20, 6 Jun 1956, *Redfearn* 2194 (FSU, GH). HAMILTON CO.: 2 mi E of Jasper, 1 May 1959, *Godfrey* 58508 (FSU). HIGHLANDS CO.: Bear Point, Lake Childs, 10 Mar 1945, *Brass* 14779 (GH). HOLMES CO.: U.S. 90, 0.2 mi E of Florida 81 in Ponce de Leon, 1 May 1968, *Stone* 2589-2591 (DUKE, NY). INDIAN RIVER CO.: St. Johns River, 10 mi W of Vero Beach, 22 Feb 1957; *Lemaire* 149 (FSU). JACKSON CO.: 2 mi E of Grand Ridge, 20 May 1960, *Godfrey* 59539 (FSU). LAKE CO.: 13 mi S of Leesburg, 10 Jun 1961, *Godfrey & Reinert* 61036 (FSU). LAKE or ORANGE CO.: Lake Apopka, 25 Apr 1930, *O'Neill-Blanton* 6442 (GH). LEE CO.: Fla. 80, 3 mi E of Tice, 15 Aug 1963, *Henderson* 63-1590 (FSU). LOWNDES CO.: 5 mi E of Valdosta, 5 May 1963, *Godfrey & Houk* 62760 (FSU). MARTIN CO.: Lake Okeechobee, Pelican Lake to Cypress Creek, 11-25 Nov 1913, *J. & G. Small* 4320 (NY). NASSAU CO.: 10 mi E of Hilliard, 23 May 1964, *Godfrey* 64093 (FSU). OKEECHOBEE CO.: Kissimmee River, N end of Lake Okeechobee, 25 Nov 1913, *J. & G. Small* 4383 (NY). PALM BEACH CO.: Loxahatchee Wild Life Refuge, W of Delray Beach, 29-30 Mar 1952, *Field & Lazar* (F, US). POLK CO.: Mountain Lake, Lake Wales, 21 Mar 1952, *Field & Lazar* (US). PUTNAM CO.: Palatka and Lake Ganoga, 18 Apr 1897 & Aug 1903, *Williamson* (PH). **Georgia.** BRANTLEY CO.: Ga. Rts. 15 & 121, 1 mi S of Hoboken, 18 Aug 1967, *Clewell* 2745 (FSU). BROOKS CO.: 1 mi NW of Morven, 6 Jun 1959, *Adams* 182 (FSU). CARLTON CO.: Near Camp Cornelia in Okefenokee Swamp, *Jarrard* 2226 (DUKE). CHATHAM CO.: Savannah, (*Pontederia*

Figure 15. Distribution of *Pontederia cordata* var. *cordata* (dots), var. *lancifolia* (triangles) and var. *ovalis* (stars) in South America.

lanceolata Nutt.), (PH). CLINCH CO.: Dupont, 4 10 1935, *Louett* (DUKE). DEKALB CO.: Lakes, 24 May 1897, *Eggert* (MO). DOOLY CO.: Vienna, Apr 1845, *Rugel* 24 (MICH). ECHOLS CO.: Ga. Rt. 94, 5 mi NW of Statenville, 17 Aug 1967, *Clewell* 2528 (FSU). GLYNN CO.: 7 mi NW of Brunswich, hwy. 341, 16 Apr 1961, *Wright* 41 (GH). LOWNDES CO.: Valdosta, 4 10 1938, *Baker* 2978 (DUKE). RICHMOND CO.: Tubman Home, Augusta, 13 Jun 1924, *Hildebrand* (DUKE). WARE CO.: Between Waycross and Ruskin, 2 Aug 1902, *Harper* 1469 (F, GH, MO, NY, US). WAYNE CO.: Jesup, 4 Jun 1893, *Kearney* (OS). **Indiana.** LAKE CO.: Miller, 24 Jun 1896, *Umbach* (PH). **Maine.** OXFORD CO.: Roxbury Pond, Byron, 20 Jul 1934, *Reed* 440 (DUKE, PH). **Massachusetts.** MIDDLESEX CO.: Fresh Pond, Cambridge, *Ball* [in part] (MO). WORCESTER CO.: East Templeton, 28 Jul 1886, *Partridge* (BKL). **Michigan.** SCHOOLCRAFT CO.: Indian Lake, 25 Jun 1937, *Beckman* 32 (MICH). **New Hampshire.** CARROLL CO.: Chocorua Lake, Tamworth, 3 Aug 1947, *Steele* (NEBC). **New Jersey.** MORRIS CO.: Green Pond, 1 Aug 1894, *Van Sickle* (BKL). **Rhode Island.** WASHINGTON CO.: Exeter, Ieppican Pond, 22 Sep 1920, *Graves & Woodward* (GH, NEBC). **South Carolina.** COLLECTON CO.: 8 mi SE of Walterboro, 18 Jul 1927, *Wiegand & Manning* (GH). SUMTER CO.: Sumter vic., 25 May 1914, *Stone* 438 (PH). **Tennessee.** COCKE CO.: Newport to Greenville, 5 mi E of Newport, 17 Jun 1939, *Sharp & Jennison* 342 (BKL,MO). COFFEE CO.: S of Manchester, 21 Aug 1938, *Svenson* 8775 [in part] (BKL, GH, PH). **Texas.** CHAMBERS CO.: Anahuac, 16 May 1937, *Cory* 22410 [in part] (GH). HARRIS CO.: Cob Pond, Humble, 9 10 1926, *Tharp* 4314 (US). WEST INDIES. **Cuba.** PROV. PINAR DEL RIO, Coloma vic., 28 Feb-2 Mar 1911, *Britton & Cowell* 9693 (GH, NY, US); Cienaga de Zapata, N de la Bahia de Cochinos (Sta Clara), 14 Aug 1920, *Leon & Loustalot* 9530 (NY); PROV. PINAR DEL RIO, near La Coloma, 1 May 1940, *Leon, Victorin & Alain* (GH); Plantae Cubenses Wrightianae, 1860-1864, *Wright* 3260 (GH, MO, NY, US). SOUTH AMERICA. **Argentina.** PROV. BUENOS AIRES, Buenos Aires, Jan 1852, *Andersson* (US); PROV. CORRIENTES, Dept. Ituzaingo, Salto Apipe, 6 X 1949, *Schwarz* 8130 (MO, US). **Brazil.** PARANA, Desiro Ribas, 29 Nov 1910, *Dusen* 10849 (GH, NY, US); PROV. MINAS GERAIS, Brasilia, cidade de Caldas, 1868, *Henschen* (US); Rio Grande Do Sul, Belem Novo, Costa Rio Guahyba, 31 Jan 1948, *Palacios & Cuezzo* 416 (MO); Rio De Janeiro estado, municipio Cabo Frio, Cabo Frio, Praia do Pontal, 17 Apr 1952, *Smith* 6595 (US). **Colombia.** COMMISSARIA MAGDALENA, Poponte, Magdalena Valley, 2 Nov 1924, *Allen* 786 (F, MO); COMMISSARIA PUTUMAYO, Umbria, Dec 1930, *Klug* 1877 (F, GH, MICH, MO, NY, US). **Paraguay.** Iter ad Paraguariam septentrionalem, superioris fluminis Apa, 1901-1902, *Hassler* 7849 (GH, MICH, MO, NY). **Uruguay.** Nueva Palmina [?] (Dto. Colonia), XII 1943-I 1944. *Scolnik* 32 (NY).

This lanceolate to narrowly linear-lanceolate leaved variety (Fig. 13) has a geographically distinct distribution in the southeastern portion of the United States (Fig. 11). The leaf width is quite variable. The extremely ovate-lanceolate forms, suggestive of hybridization, are predominant throughout the overlapping ranges of this variety and *P. cordata* var. *cordata*.

1c. *Pontederia cordata* L. var. *ovalis* (Mart. in Roemer & Schultes) Solms in DC., Monog. Phan. **4**: 533. 1883.

Pontederia ovalis Mart. in Roemer & Schultes, Syst. Veg. **7**: 1140. 1830. [Martius, Fl. Bras. 3(1): 95. 1847.] Type: Brazil (Holotype M; photograph of holotype US!).

Pontederia lanceolata Nutt. var. *vichadensis* Hermann, Caldasia **5**: 39. 1948. Type: Colombia: Vichada, mucky edge of stream in open forest on llanos bordering the Rio Vichada, alt. 100 m, ca. 18 km NE [E.N.E.] of San José de Ocuné, 21 Jan. 1944, *F. J. Hermann* 11045 (Holotype US!).

Pontederia lanceolata Nutt. forma *ovalis* (Mart. in Roemer & Schultes) Castell., Rio de Janeiro Jardin Botanico **15**: 62. 1958.

Plants up to 9 dm tall. Leaves ovate (Fig. 14), blades 2.2-21 cm wide; spathe (terminal phyllode of floral shoot 2.2-7.4 cm long; petiole of floral shoot leaf (Fig. 14, includes sheath base) 5.3-31 cm long; petiole of other leaves 28.7-30.6 cm long, ligule of petiole sheath up to 4 cm long; sheath in axil of floral shoot up to 22.3 cm long. Inflorescence 2.7-16 cm long; peduncle (inflorescence base to floral shoot leaf base) 12.3-28 cm long, densely pubescent next to inflorescence base. Perigone white or pale blue.

In South America (Fig. 15) known only from Bolivia, Brazil, Colombia, Paraguay and Uruguay.

Representative Specimens. SOUTH AMERICA. **Bolivia.** DEPARTMENT BENI: Reyes, 27 Oct 1921, *Rusby* 1389 (BKL, GH, MICH, NY, PH, US). **Brazil.** Prov. Minas Gerais, Dattos de Cima, Mun. Diamantina, 19 Nov 1937, *Barreto* 9817 (F); Rio Grande Do Sul, Neu. Wurhemburg, 10 11 [19]04, *Bornmuller* 356 (GH); *Burchell* A157 (GH); *Burchell* A163 [in part] (GH); 12 km S of Cristaes, Ceara, 28 Aug

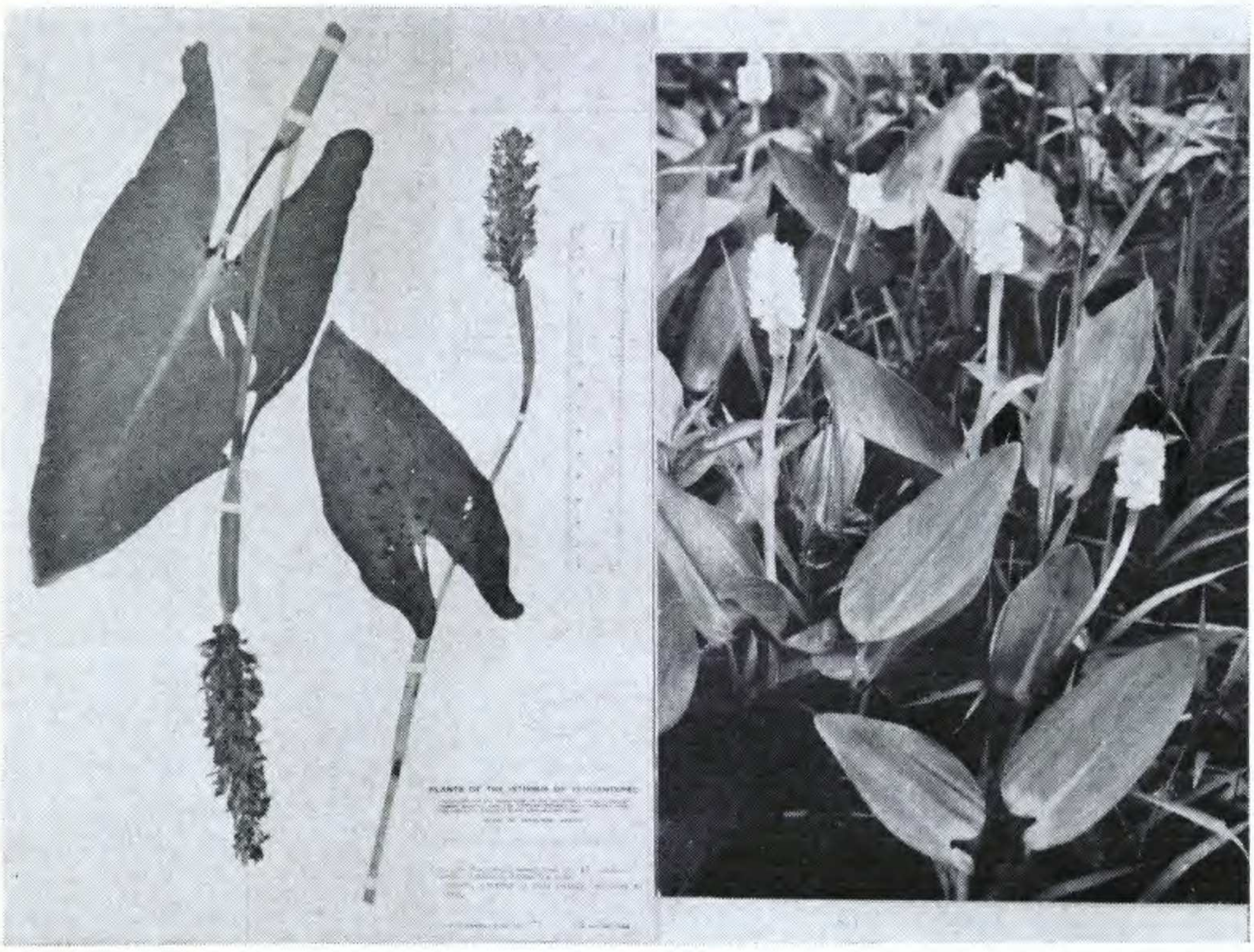

Figure 17. *Pontederia sagittata* with sagittate auricled flowering stalk leaves, Mexico, State of Vera Cruz, *R. M. King* 933 (US); at left.

Figure 18. White inflorescences of *Pontederia parviflora*, with subcordate leaves, Panama, Province of Herrera (*Lowden* photo, Aug 1970); at right.

Miramar, 19 Mar 1955, *Sohns* 1658 (MICH, NY, US). STATE OAXACA: Jamiltepec, Distrito Jamiltepec, Oaxaca, 10 Dec 1921, *Conzatti* 4434 (NY); Chiltepec and vic., District Tuxtepec, Jul 1940-Feb 1941, *Martinez-Calderon* 76494 (GH, US); Near San Gabriel Mixtepec, Mpio. de Juquila, 2 km N San Gabriel, 13 Feb 1965, *McVaugh* 22416 (MICH);Laguna Tonameca, Oaxaca, 8 Nov 1917, *Reko* 3451 (US); Foothills Sierra Madre del Sur, 53 km N of Puerto Escondido, road to Zimatlan km 221, 25 Jul 1965, *K. & E. Roe & Mori* 559 (F, WIS). STATE TABASCO: Popal Grande between Frontera and Villahermosa, Aug 1962, *Barlow* (MICH, WIS); W-SW of Huimanguillo, 23 May 1963, *Barlow* 30/52 (WIS); La Palma, Balancan, 1-6 Jun 1939, *Matuda* 3302 (GH, MICH); Curahueso, Tabasco, 6 Jan 1889, *Revirosa* 334 (NY, PH). STATE VERA CRUZ: Wartenberg, near Tantoyuca, prov. Huasteca 1858, *Ervendberg* 277 (GH, PH); Vera Cruz, 12 Aug 1926, *Fisher* 108 (US); prov. Vera Cruz, *Galeotti* 5562 (F, GH, NY, US); Mun. Puente Nacional, km 394 Jalapa-Vera Cruz highway, between Rinconada and Puente Nacional, 13 Feb 1943, *Gilly, Simpson & Dodds* 90 (MICH); Near city Vera Cruz, 23 Jan 1906, *Greenman* 19 (F, GH); Vera Cruz, in and around, 8 Dec 1958, *Jones* 22660 (WIS); Trans-Isthmian highway Route 185, 17 km NE of Minatitlan, 1 Aug 1958, *King* 933 (MICH, US); *Vera Cruz, El Coyol, Prolongacion Carretera Aleman, 25 Jul 1970, *Lowden* 6 (OS); Carretera Nacional 180, El Puente Teculapilla, 5 km NW of Lerdo Route 180, 26 Jul 1970, *Lowden* 7 (OS); Laguna Catemaco, S edge off Route 180, 27 Jul 1970, *Lowden* 8a-b (OS); Laguna Catemaco, Arroyo Agrio, 6 km from Catemaco Town between Coyame and San Andres Tuxtla, 27 Jul 1970, *Lowden* 9 (OS); Vera Cruz, A° 1853, *Müller* 2145 (NY); Jalapa, 16 Feb 1910, *Orcutt* 2874 (F, GH, MO, US); Barranca de Panoaya, Mar 1923, *Purpus* 9041 (F, GH, MO, NY, US); Rio Maquina, municipio San Andres Tuxtla, 26 Mar 1964, *Quintero* 699 (MICH); Rio Los Tuxtla, municipio Santiago Tuxtla, 29 Aug 1964, *Quintero* 1409 (MICH); Sontecomapan, municipio Catemaco, 5 Aug 1965, *Rzedowshi* 20368 (MICH); Rio Cosolapa, Le Gartera, Ejido San Agustin, 5 km NE of Campo Experimental de Hule, El Palmar, Zongolica, 27 Feb 1944, *Santos* 2821 (MICH); Vera Cruz, inter urbem et Santa Fe et prope los Cocos, Feb, *Schiede & Deppe* 981 (MO, US); Coatzacoalcos, isthmus Tehuantepec, 8 Jan 1895, *Smith* 1034 (F, GH, MICH, MO, NY, US, WIS); Tuxpam [Tuxpan], Rio Vinasco [Rio Vinazco], 9 I 1903, Ex Museo botanico Berolinensi 3731 (GH, US); Distr. San Andres Tuxtla, Laguna Catemaco, 7 III 1907, Ex Museo botanico Berolinensi 5005 (GH). STATE ?: Winter 1877, *Hogg* (NY); San Luis, 27 Feb 1899, *Langlasse* 928 (GH, US); Inter el Morro & Rancho Nuevo, 1841-43, *Liebmann* 1618 (US). CENTRAL AMERICA. **Costa Rica.** PROVINCE LIMON: Matina, IX 1896, *Pittier* 10301 (US). **Guatemala.** DEPARTMENT ALTA VERAPAZ: Coban, M Dec 1886, *Türckheim* 547 (GH, NY, PH, US); Cubilquitz [Gubilquitz], M Apr 1901, *Tüerckheim* 8025 (US). DEPARTMENT IZABAL: Izabal, Rio Mosinga, 2 Jun 1919, *Blake* 7864 (GH, US); Jocolo, Izabal, Lago Izabal, 25 Dec 1920, *Johnson* 1053 (US); Lago Izabal, Izabal vic., 1 May 1966, *Jones & Facey* 3213 (F, NY); Livingston, 18 Jan 1905, *Kellerman* 5131 (OS, US); Quirigua, 31 Jul 1970, *Lowden* 10 (OS). Puerto Barrios, 1 Aug 1970, *Lowden* 11 (OS); Puerto Barrios vic., 29 Dec 1904, *Maxon & Hay* 3061 (US); Rio Dulce, 15 May 1937, *Muenscher* 12623 (F); Livingston, 27 May 1905, *Pittier* 357 (NY, US); Rio Dulce, M Mart 1889, *Smith* 1652 (GH, US); Quirigua vic., 15-31 May 1922, *Standley* 24029 (GH, NY, US); Puerto Barrios vic., 2-6 Jun 1922, *Standley* 25005 (US); near Quirigua, 26-27 Apr 1939, *Standley* 72425 (F); Near Puerto Barrios, 25 Apr-6 May 1939, *Standley* 73170 (F); Between Bananera and La Presa in Montana del Mico, 28 Mar 1940, *Steyermark* 38050 (F, US); Lago Izabal, opp. San Felipe, between San Felipe and mouth of Rio Juan Vicente, 19 Apr 1940, *Steyermark* 39688 (F). DEPARTMENT SAN MARCOS: Rio Suchiate, W of Ayutla, 18 Mar 1940, *Steyermark* 38034 (F). DEPARTMENT PETEN: El Paso, San Pedro River, 26 Apr 1932, *Lundell* 1564 (MICH, NY). DEPART-

MENT ZACAPA: Gualan, 15 Jan 1905, *Deam* 208 (F, GH, MICH, MO, NY, US). DEPARTMENT ?: Feb 1912, *Cockerell* 10 (US); Eastern portions of Vera Paz and Chiquimula, 1885, *Watson* 28, 33, 386 (GH). **Honduras.** DEPARTMENT ATLANTIDA: Ceiba, 26 Sep 1916, Dyer A92 (US); Tela, La Curva, 10 Aug 1970, *Lowden* 15 (OS); Santiago, 11 mi W of Tela, 10 Aug 1970, *Lowden* 16 (OS); La Ceiba, Platanillo, 6 Nov 1948, *Molina & Becker* 1 (F); Tela, 1923, *Severen* 5 (US); Tela vic., 14 Dec 1927-15 Mar 1928, *Standley* 53607 (F, US); Tela River, (Tela) Puerto Sierra, 18 Jan 1903, *Wilson* 70 (F, NY, US); Near Micos Lagoon, 12 km W of Tela, 21 Jul 1934, *Yuncker* 4684 (F, MICH); Ceiba vic., 6 Jul 1938, *Yuncker, Koepper & Wagner* 8249 (F, GH, MICH, MO, NY, US). DEPARTMENT CORTES: Puerto Cortes, 3 Ave-5 Calle 0, 9 Aug 1970, *Lowden* 13 (OS); 13.5 mi inland from Puerto Cortes along main road, 9 Aug 1970, *Lowden* 14 (OS); San Pedro Sula, Depart. Santa Barbara, M Mart 1889, *Thieme* 5510 (GH, US).

Specimens for which identification is not positive. **Guatemala.** DEPARTMENT ALTA VERAPAZ: Route 5, between Semococh and La Laguna, road to Chajmayic, 10 May 1942, *Steyermark* 46362 (F). DEPARTMENT PETEN: Isabilito, 28 Mar 1932, *Lundell* 1445 (MICH, US); El Paso, San Pedro River, 26 Apr 1932, *Lundell* 1564 (US); Santa Teresa, Subin River, 10 Apr 1933, *Lundell* 2709 (F, MICH); Laguna Peten Itza, frente Playa Blanca, Santa Elena, 3 Jan 1970, *Ortiz* 512 (F).

The smooth ridged hardened perigone bases (Fig. 1B) easily distinguish this species. The collection in Costa Rica (Fig. 16) reflects a more continuous distribution along the Caribbean Coastal Plain. Specimens without positive identification are immature vegetative specimens lacking mature perigones.

3. *Pontederia parviflora* Alex., N. Am. Flora **19**: 59. 1937. Type: Panama: Province of Panama, camino del Boticario, near Chepo, altitude 30 to 50 meters, October 1911, *H. Pittier* 4556 (Holotype NY!; isotype US!). Fruiting specimen cited with holotype, Panama, Province of Cocle, Aguadulce, in savannas, near sea level, 3-6 December 1911, *H. Pittier* 4915 (GH!, NY!, US!).

Pontederia cordata L. var. *parviflora* (Alex.) Schery, Ann. Missouri Bot. Gard. **31**: 156. 1944.

Plants (Fig. 18) up to 7 dm tall. Leaves (Fig. 18) subcordate, blades 1.8-10.5 cm wide; spathe (terminal phyllode

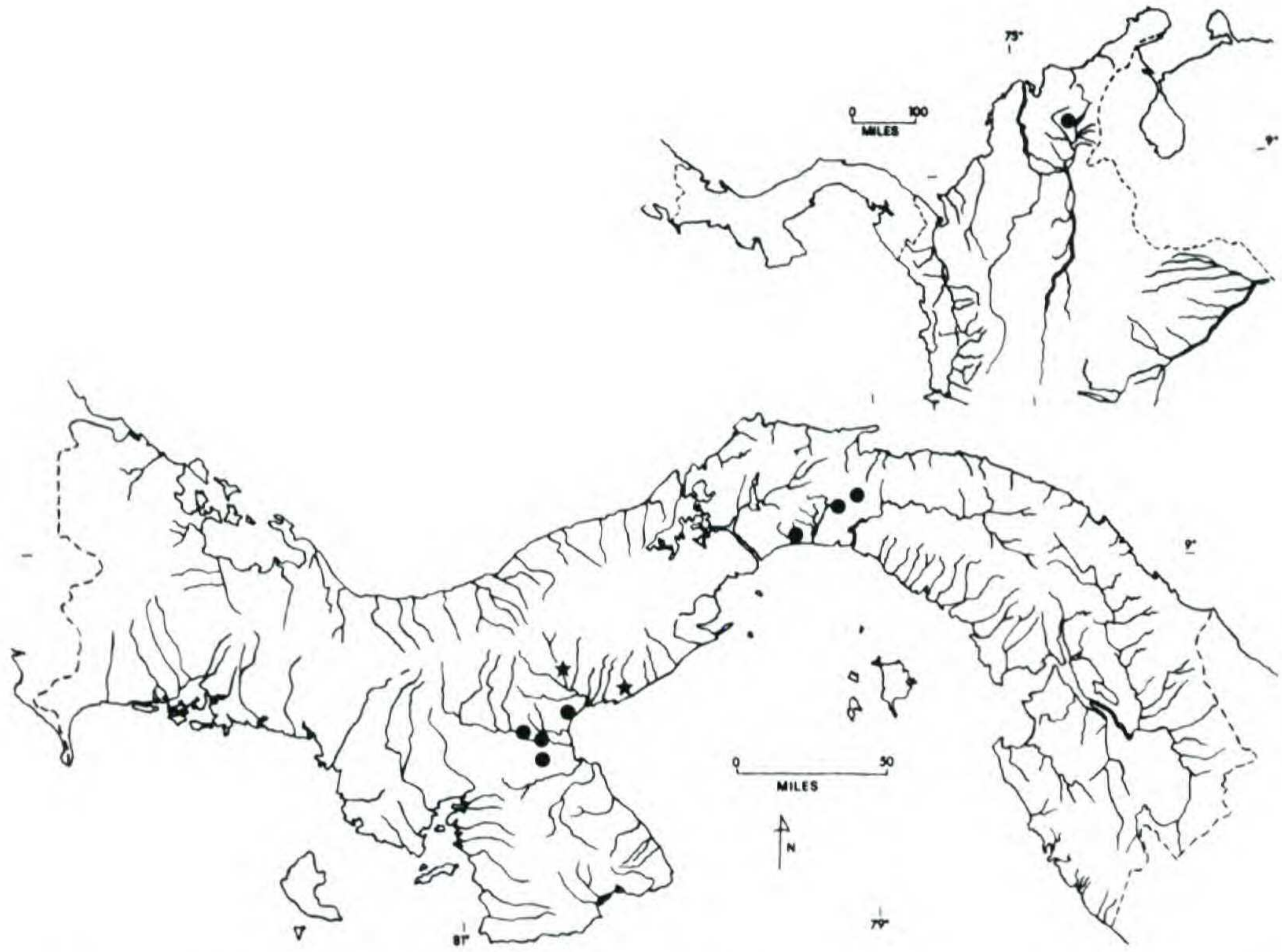

Figure 19. Distribution of *Pontederia parviflora* in Panama and Colombia (stars represent sighted records).

of floral shoot) 5-10.5 cm long; petiole of floral shoot leaf (includes sheath base) 5.5-19 cm long; petioles of other leaves 19-45 cm long; sheath in axil of floral shoot up to 34 cm long. Inflorescence 3-9.5 cm long, peduncle (inflorescence base to floral shoot leaf base) 21-35 cm long. Perigone white to white green; hardened perigone bases (Fig. 1C) toothed ridged; anthers brown to black. Homostylous (Fig. 3D). Fruits and seeds (Fig. 2A-B) reniform.

Known only from the Pacific coast of Panama, Golfo de Panama and the Caribbean Coast of Colombia. Figure 19.

Specimens Examined. CENTRAL AMERICA. **Panama.** PROVINCE COCLE: Aguadulce, 3-6 Dec 1911, *Pittier* 4915 (GH, NY, US); Between Aguadulce and Anton, 12 Jul 1938, *Woodson, Allen & Seibert* 1208 (GH, MICH, MO, NY). PROVINCE HERRERA: Santa Maria, 13 Sep 1938, *Allen* 790 (MICH); Near Divisa, 10 Aug 1962, *Dwyer* 2468 (US); Santa Maria and El Escota, 24 Aug 1970, *Lowden* 20 (OS). PROVINCE PANAMA: Between Panama and Chepo, 29 Nov 1934, *Dodge, Hunter, Steyermark & Allen* 16702 (MICH, MO); Between Pacora and Chepo, 7 mi from Chepo, Tapagara, 26 Aug 1970, *Lowden* 21 (OS); Camino Boticario, near Chepo, Oct 1911, *Pittier* 4556 (NY, US); Swamp E of Rio Tecumen [Rio Tocumen], 11 Dec 1923, *Standley* 26495, 26656 (US); Between Pacora and Chepo, 1 Aug 1938, *Woodson, Allen & Seibert* 1661 (GH, MICH, NY). SOUTH AMERICA. **Colombia.** DEPARTMENT MAGDALENA: Rio de Hacha, near Molino, Sa. Martha, Pur[chi], 1845, Hooker; Costa Del Caribe, oeste de Los Venados, 31 Sep 1961, *Dugand* 5834 (US).

This is the only homostylous member of the genus. Its unique style form (Fig. 3D), white inflorescence (Fig. 18) and brown-black anthers distinguish *Pontederia parviflora* from other members of subgenus *Pontederia.* A wider distribution is expected in South America.

II. *Pontederia* subg. *Reussia* (Endl.) Lowden, comb. nov. *Reussia* Endl. (nom. cons.), Gen. Pl. 139. 1836. Type *Reussia triflora* Seub. in Mart. Fl. Bras. 3 (1): 96. 1847.

Hardened perigone bases (Fig. 1D) spinulose ridged; floral bearing shoots prostrate; aerial stems with long internodes; underground rhizomes short (mature plants).

Subgenus *Reussia* reaches its northern limits in British Honduras and extends into South America as far south as east central Argentina.

4. *Pontederia rotundifolia* L. f., Suppl. 192. 1781. Type: Surinam, *C. G. Da*[h]lberg (Lectotype chosen, [Savage, 407.2], LINN).

Pontederia cordifolia Mart. in Roemer & Schultes, Syst. Veg. 7: 1142. 1830. Type: Brazil: "Crescit in Brasiliae mediterraneae stagnis" (Holotype M; photographs of holotype NY!, US!).

Pontederia brasiliensis Willd. Roemer & Schultes, Syst. Veg. 7: 1145. 1830. Type: Brazil: "In Brasilia prope Para. Com. de Hoffmannsegg". Type not seen.

Unisema orbiculata Raf., Med. Fl. 2: 108. 1830. Type based on the type of *P. rotundifolia* L. f.

Pontederia eriantha Miquel, Linnaea 17: 60. 1843. Type: Surinam: "Crescit Surinami, ad ripas fluminis Commewyne, *Focke*" (Holotype GH!).

?*Pontederia renniformis* Larranaga, Pub. Inst. Hist. Geog. Uruguay 2: 134. 1930. Type not indicated.

Figure 20. Inflorescence of *Pontederia rotundifolia*, showing a bilobed spot on the largest perianth lobe, El Salvador, Laguna de Zapotitan (*Lowden* photo, Mar 1970); at left.

Figure 21. Reniform leaves and short inflorescence of *Pontederia rotundifolia*, Brazil, Territory of Rondonia, *Prance, Forero, Wrigley, Ramos & Farias* 5914 (NY); at right.

Reussia grazielae Machado, Revista Brasil. Biol. 7: 177. 1947. Type: "Amazonas Bahia, in acquis, 1937, *Ducke* 55083 (Holotype RB; photograph of holotype, Machado 1947, Fig. 3).

Reussia rotundifolia (L. f.) Castell., Lilloa 25: 593. 1951.

Plants up to 12 dm tall. Leaves reniform (Fig. 21), sagittate (sometimes deeply auricled) or cordate; blades 3.2-22 cm wide; spathe (terminal phyllode of floral shoot) 2.5-4.5 cm long; petiole of floral shoot leaf (includes sheath base) 4.7-45 cm long; petiole of other leaves 17-54 cm long, ligule of petiole sheath up to 7.5 cm long; sheath in axil of floral shoots up to 24 cm long. Inflorescence (Fig. 20) 2-7.5 cm long, peduncle (inflorescence base to floral shoot leaf base) 6-25 cm long. Perigone pale blue or blue; hardened perigone bases (Fig. 1D) spinulose ridged; anthers blue. Tristylous (Fig. 3A-C). Fruits and seeds (Fig. 2C-D) ovoid.

In Central America (Fig. 22) a more frequent inhabitant of highland lagoons and lakes than the coastal plains. In South America (Fig. 25) primarily a floristic component of the tributaries of the Amazon Basin.

Specimens Examined. CENTRAL AMERICA. **British Honduras.** TOLEDO DISTRICT: Monkey River, 9 Oct 1941, *Gentle* 3700 (F, GH, MICH, MO, NY, US). **Costa Rica.** PROVINCE ALAJUELA: Lago near Los Chiles, Rio Frio, 1 Aug 1949, *Holm & Iltis* 823 (GH). PROVINCE GUANACASTE: 1 km from Arenal, 2 km from Tronadora, 18 Aug 1970, *Lowden* 19 (OS); Rio Arenal, 5 V 1923, *Valerio* 4 (US); Arenal, 5 IX 1923, *Valerio* 360 (US). PROVINCE LIMON: Barro Colorado de Norte, 8 Mar 1965, *Blaisdell* 267 (FSU); Finca Montecristo, Rio Reventazon below Cairo, 18-19 Feb 1926, *Standley & Valerio* 49024 (US). **El Salvador.** DEPARTMENT LA LIBERTAD: Laguna Zapotitan, 9 Nov 1953, *Fassett* 29320 (MO, WIS); *Laguna Zapotitan, 26 Mar 1970, *Lowden* 23 (OS). DEPARTMENT SAN SALVADOR: San Salvador, 1922, *Calderon* 411 (NY, US); Asino, W end of Lago Ilopango, 30 Oct 1950, *Fassett* 28364 (F, MO, US, WIS); Asino, W end of Lago Ilopango, 8 Jan 1951, *Fassett* 28582 (F, GH, US, WIS); San Salvador vic., 1905, *Renson* 273 (NY, US); Lago Ilopango, W Seite, bei Asino, 7 1 1951, *Rohweder* 566 (F); San Salvador vic., 20 Dec 1921-4 Jan 1922, *Standley* 19143 (GH, NY, US); San Salvador vic., 30 Mar-24 Apr 1922, *Standley* 23284 (GH, US). **Guatemala.** DEPARTMENT ALTA VERAPAZ: Panzos, 19 Nov 1920, *Johnson* 1028 (F, US); Panzos, 1 May 1906, *Lewton* 400 (US). DEPARTMENT IZABAL: Izabal, Rio Izabal, 1 Jun 1919, *Blake* 7844 (GH, US). **Honduras.** DEPARTMENT COMAYAGUA: Pito Solo, Lake Yojoa, 3 Sep 1932, *Edwards* AQ1 (F, GH); *Pito Solo, Lake Yojoa, 8 Aug 1970, *Lowden* 12 (OS); Pito Solo, Lago Yojoa, 18 Apr 1945, *Rodriguez* 2917 (F); Cortez, Lake Yojoa, 7 Jul 1943, *Yuncker* 4840 (F, MICH, MO). DEPARTMENT CORTES: Agua Azul tract No. "B", Lake Yojoa, 16 Aug 1951, *Kamb* 2094 (GH). **Nicaragua.** DEPARTMENT GRANADA: Granada, 11 Feb 1903, *Baker* (GH, MO, NY); Granada, Lake Nicaragua, *J. M. & M. T. Greenman* 5746 (MO); *Granada vic., la Terraza, Lago Nicaragua, 14, 16 Aug 1970, *Lowden* 17 & 18 (OS). DEPARTMENT ?: U.S. North Pacific Exploring Expedition, 1853-56, *Wright* (GH, US). **Panama.** CANAL ZONE: Rio Chagres, near Gamboa, 25 Aug 1939, *Allen* 1963 (GH, MICH, MO); Barro Colorado Island, Jan 1939, *Brown* 30 (F); Ahorca Lagarto to Culebra, 9 Mar 1905, *Cowell* 379 (NY); Frijoles, 17 Jun 1960, *Ebinger* 69 (MO); Barro Colorado Island, near dock, 28 Jun 1960, *Ebinger* 209 (MO, US); Barro Colorado Island, 23 Dec 1963, *Graham* 212 (GH, MICH); Gatun Lake, Jul 1965, *Hayden* 123 (MO); Gatun Station, Panama Railroad,

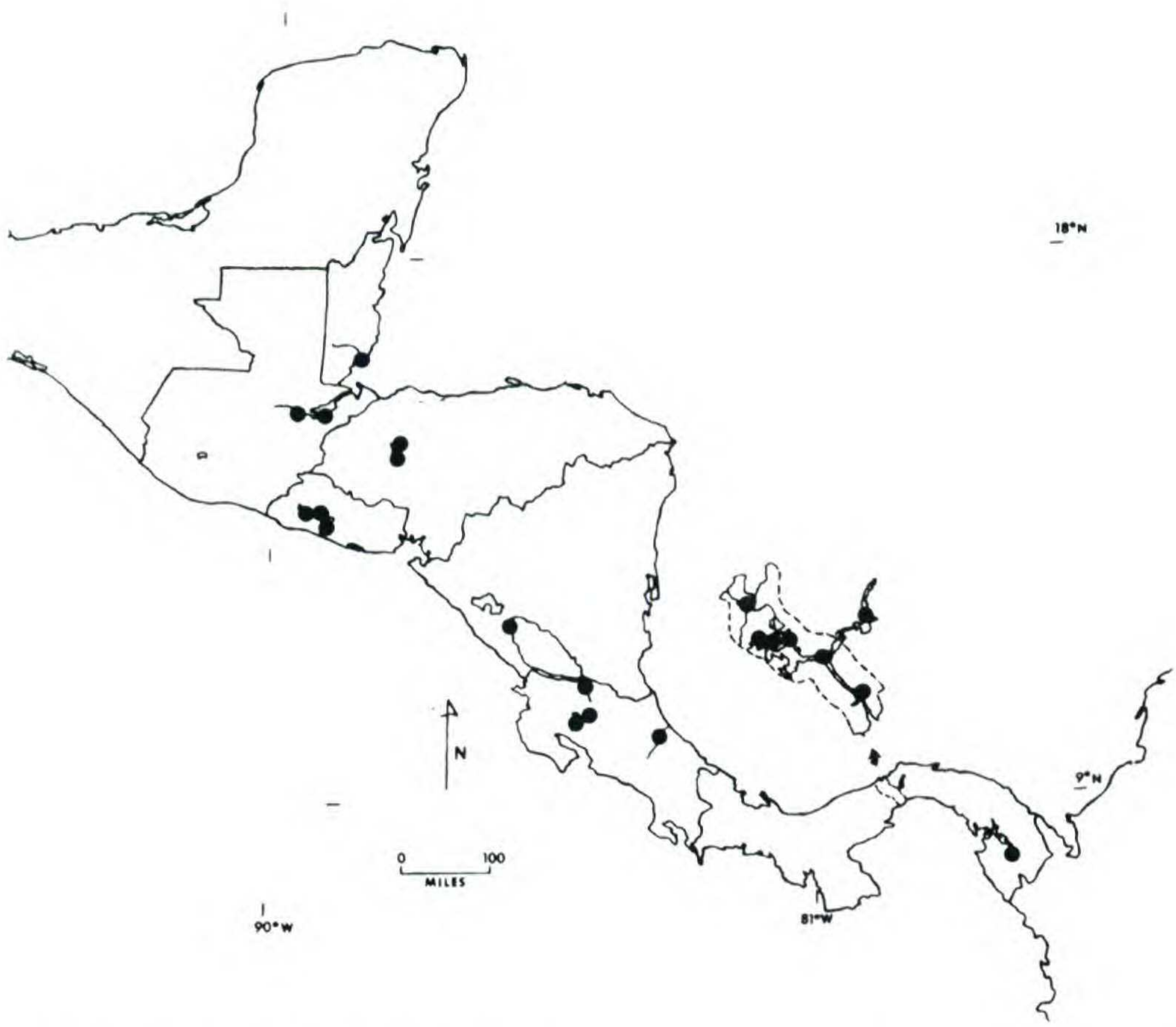

Figure 22. Distribution of *Pontederia rotundifolia* in Central America (arrow points to insert of Canal Zone).

28 Oct 1859, *Hayes* 89, 93 (GH) and 99 (NY); Miraflores Lake, Empire, Culebra Cut and vic., 27 Feb 1935, *Hunter & Allen* 776 (MO); Barro Colorado Island, 24 Jul 1927, *Kenoyer* 602 (US); Chagres River, N of Gamboa, 2 Jun 1969, *Lazor, Correa & Boreham* 3739 (FSU); Chagres River below Gatun, 17 Feb 1911, *Maxon* 4883 (US); Between Gatun and Lion Hill, 26 Jan 1911, *Pittier* 2572 (GH, NY, US); Barro Colorado Island, Barbour Trail, 15 Nov 1931, *Shattuck* 408 (F); Barro Colorado Island, Pena Blanca Bay, 31 Jul 1934, *Shattuck* 1099 (F, MO); Barro Colorado Island, *Starry* 120 (F); Barro Colorado Island boathouse, 25 Jun 1966, *Tyson* 4198 (FSU, MO); Gamboa, 14 Jul 1966, *Tyson, Dwyer & Blum* 4604 (FSU, NY, US); Barro Colorado Island, Chapman Trail, 28 Feb 1931, *Wilson* 74 (F); Madden Lake, 3-20 Aug 1940, *Woodson & Schery* 949 (MO, NY, US); Barro Colorado Island, W of end of T. Barbour Trail, 11 Feb 1932, *Woodworth & Vestal* 479 (F, GH). PROVINCE DARIEN: Rio Pirre, Apr 1966, *Duke & Bristan* 8307 (MO). SOUTH AMERICA. **Argentina.** Entre Ensenada and Punta Lara, Prov. Buenos Aires, La

Plata, 2 Apr 1931, *Cabrera* 1708 (NY); Buenos Aires, Rio Santiago, Prov. Corrientes, 18 Apr 1964, *Cabrera* 15915 (NY); Camino de Santa Fe, Laguna Stubal's Guadalupe, Prov. Santa Fe, 1 II 1936, *Job* 679 (NY); Estancia "Santa Teresa", Dep. Mburucuya, Prov. Corrientes, 2 4 1954, *Petersen* 2657 (MO, US); Prope Barra, Prov. Rio Negro, May 1851, *Spruce* 1486 (NY). **Bolivia.** DEPARTMENT BENI: Lake Rogagua, 3 Nov 1921, *Cardenas* 1417 (BKL, MICH, NY, US); Rio Chapare-Mamore, VIII 1926, *Werdermann* 2198 (MO); Reyes, 25 Oct 1921, *White* 1513 (BKL, NY). DEPARTMENT LA PAZ: Ixiamas, 21 Dec 1921, *Cardenas* 2031 (BKL, MICH, NY). DEPARTMENT SANTA CRUZ: Yapacani, VI 1892, *Kuntze* (NY); Prov. Para, 6 Feb 1925, *Steinbach* 6977 (GH). **Brazil.** STATE AMAZONAS: Basin Rio Madeira, municipality Humayta, between Monte Christo and Santa Victoria, Rio Ipixuna, 15-17 Nov 1934, *Krukoff* 7129 (F, GH, MICH, MO, NY, US). STATE PARA: Belem, Mar-May 1929, *Dahlgren & Sella* 525 (F, US), 557 (F, GH); Villa Carmo, municipio Cameta, 4 Jul 1935, *Drouet* 1999 (GH, MICH, US); Taperinha bei Santarem, Amazonas armes Ayaya, II VI 1927, *Ginzberger & Zerny* 757 (F); Rio Parana, Barra do Rio Piquiry, State of Parana, Mun. Guaira, 9 IV 1961, *Hatschbach* 8078 (US); Bocca do Paru, Region Lower Amazon, 28-29 Aug 1934, *Krukoff* 5935 (GH, NY); Amazonia, 28 Sep 1945, *Pires & Black* 770 (GH); Amazonia, Territory Rondonia, Basin Rio Madeira east bank at Abuna, 12 Jul 1968, *Prance, Forero, Wrigley, Ramos & Farias* 5914 (NY, US); Amazonia, Territory Rondonia, Basin Rio Madeira, Rio Pacaas Novos, 3 Aug 1968, *Prance, Forero, Wrigley, Ramos & Farais* 6764 (NY, US). **Colombia.** Frontera Colombo-Ecuatoriana, commissaria Putumayo, rio San Miguel entre los aflu-entes Bermeja y Conejo, 13 Dec. 1940, *Cuatrecasas* 11054 (F, US); Mocoa, camino de herradura antiquo y rio Rumiyaco, 10 Oct 1965, *Garcia-Barriga, Hashimoto & Ishikawa* 18685 (NY); Amazonas, Trapecio Amazonico, Loretoyacu River, Nov. 1945, *Schultes* 6935 (US); Amazonas, Trapecio Amazonico, Amazon River, Leticia, Sep 1946, *Schultes* 8188 (US). **Guiana.** Martin, Ex Herbario Musei Britannici (F). **Paraguay.** Lag. Ypacaray, 1885-1895, *Hassler* 1196 (NY); Lacus Ypacarai, Dec 1900, *Hassler* 3693 (NY); Lacus Ypacarai regione, 1913, *Hassler* 11861 (F, GH, MO, NY, US); San Bernardino, Dept. Cordillera, 4 II 1951, *Sparro & Vervoorst* 2316 (GH); Apr-May 1845, *Weddell* 3156 (NY). **Peru.** DEPARTMENT LORETO: Requena, Prov. Requena, Ucayalio Fangoso, 22 Aug 1965, *Sagastequi & Aldave* 5757 (US); Pebas, Amazon River, 29 Jul 1929, *Williams* 1854 (F); La Victoria, Amazon River, 5 Sep 1929, *Williams* 3097 (F, US). **Surinam.** *Focke* (GH); Via secta ab Wia-bank and Grote Zwiebelzwamp, 23 Nov 1948, *Lanjouw & Lindeman* 1236 (NY). **Venezuela.** Pto. de La Ceiba, sur lago de Maracaibo, Edo. Trujillo, Jan 1961, *Aristeguiseta* 4443 (US); C. Araguo [Boca Araguao], State Delta Amacuro, Dec 1952, *Gines* 4881 (US); 12 km SW of

Punta de Piedra towards Sacramento, Estado Tachira, 27-30 Aug 1966, *Steyermark & Rabe* 96610 (US).

This vigorous species is quite variable in size and leaf forms. In particular, specimens with sagittate leaves have been confused with *Pontederia sagittata.* The spinulose hardened perigone bases (Fig. 1D) and fewer flowered globose inflorescences (Fig. 20) readily distinguish *P. rotundifolia* from members of subgenus *Pontederia.*

5. *Pontederia subovata* (Seub. in Mart.) Lowden, comb. nov.

Eichhornia subovata Seub. in Mart. Fl. Bras. 3 (1) : 91. 1847. Type: Brazil: Prov. Goyazana, 1836-1841, *Gardner* 4022 (Lectotype chosen, NY!) ; prov. Bahiensi, *Blanchet* 2720.

Reussia triflora Endl. ex Seubert in Martius, Fl. Bras. 3 (1) : 96. 1847. Type: Brazil: *Pohl, Sellow.* Type not seen.

Pontederia schomburgkiana Klotzsch in Schomburgk., Vers. Faun. & Fl. v. Brit. Guiana 1118. 1848. Type: British Guiana: "Im See Venturu und auf stromlosen Stellen des Pirara in der Nähe seiner Quelle". Type not seen.

Pontederia lagoënsis Warming in Videnskab. Meddel, p. 323, T. VI. 1871. Type: Brazil: Min. Geraes, Lagoa Santa. Type not seen.

Reussia subovata (Seub. in Mart.) Solms in DC., Monog. Phan. **4:** 534. 1883.

Reussia lagoënsis (Warm.) Castell., Arq. Jard. Bot. Rio de Janeiro **16:** 209. 1958.

Plants up to 30 cm tall. Leaves subovate (Fig. 23), ovate lanceolate or elliptic (Fig. 24) ; blades 0.2-4.4 cm wide; spathe (terminal phyllode of the floral shoot) 1.9-5 cm long; petiole of floral shoot leaf (includes sheath base) 4-10 cm long; petiole of other leaves 6.5-25 cm long, ligule (Fig. 23) of petiole sheath up to 3.5 cm long; sheath in axil of floral shoot up to 6.5 cm long. Inflorescence (Fig. 23) 3-8 cm long; peduncle (inflorescence base to floral shoot leaf base) 5-14 cm long. Perigone ephemeral, blue purple,

Figure 23. Inflorescence and subovate leaves of *Pontederia subovata* (arrow points to a ligule of a petiole sheath), Paraguay, Ypacaray, *E. Hassler* 12503 (MO); at left.

Figure 24. Narrow subovate-lanceolate leaf variant of *Pontederia subovata,* Brazil, Minas Gerais, Lagoa Santa, *L. B. Smith* 6702 (US); at right.

blue green or pale blue; hardened perigone bases spinulose ridged; anthers blue. Tristylous.

Inhabits swamps and lakes of Argentina, Bolivia, Brazil, British Guiana, Paraguay and Venezuela. Figure 25.

Specimens Examined. SOUTH AMERICA. **Argentina.** Territorio de Formosa, 4 1919, *Jorgensen* 3347 (GH, US); Prov. Chaco, Loc. Colonia Benitez, 10 II 1941, *Meyer* 3864 (F, GH, NY); Estancia, "Santa Teresa", Dep. Mburucuya, Prov. Corrientes, 4 1 1952, *Petersen* 1427 (NY, US). **Bolivia.** Trinidad [Dept. of Beni], 7 Mar 1922, *Cardenas* 27 (GH, NY); Santa Cruz, Chiquitos, between El Carmen & Palmito-Chiquitos, II 1950, *Cardenas* 4488 (US); Reis, Jun 1886, *Rusby* 553 (GH, NY). **Brazil.** 1836-1841, *Gardner* 4022 (NY); Loc. S. Tereziuha, Mun. Ituiutaba, Estado Mg [Minas Gerais], 23 Apr 1950, *Macedo* 2326 (NY); Loc. S. Terezuiha, Estado Minas, Mun. Ituiutaba, 18 Feb 1951, *Marcedo* 3168 (US); Canoas, Estado do Rio Grande do Sul, 1 2 1949, *Miguel* 23 (F, GH, US); Minas Gerais, Mun. Lagoa Santa, Lagoa Santa, 3 May 1952, *Smith* 6702 (F, GH, NY, US).

Figure 25. Distribution of *Pontederia rotundifolia* (dots) and *P. subovata* (triangles) in South America.

British Guiana. Rupununi, 20 mls. S. of Lethem, road to Wichabi, 22 Nov 1957, *Cooke* 197 (NY); Twinpools South Sand Creek, *Cooke* 205 (NY); Rupununi Northern Savanna, Mauritia Swamp, ¼ mi N Waruma, 30 Sep 1963, *Goodland* 897 (US). **Paraguay.** Iter ad Paraguariam Septentrionalem, prope Concepcion, Sep 1901/2, *Hassler* 7352 (GH, NY); Paraguaria Centralis, in regione lacus Ypacaray, Feb 1913, *Hassler* 12503 (GH, MO, NY, US); Pilcomayo River, 1888-1890, *Morong* 859 (NY). **Venezuela.** State Cojedes, near San Carlos, 15 Jan 1939, *Alston* 6311 (WIS); Apure, near Cunaviche, 13 Feb 1941, *Chardon* 254 (US).

The subovate and lanceolate leaf forms are quite variable, however, distinct. The narrow almost linear-lanceolate variants (Fig. 24) are not formally treated since material studied was limited. The hardened perigone bases are spinulose ridged.

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Table 2. Chromosome Counts of *Pontederia* Taxa Investigated

Taxon	Haploid Counts	Vouchers (OS)
subg. *Pontederia*		
P. cordata var. cordata	8	U.S.: Ohio, Ottawa Co., Winous Pt., SW of Port Clinton, *Lowden* 36, 37; New Hampshire, Strafford Co., Bellamy River, *Lowden* 2. British Honduras: Belize District, 9 miles N of Belize City, Northern Highway, *Lowden* 24.
P. sagittata	8	Mexico: State Vera Cruz, Vera Cruz, *Lowden* 6, Lerdo, *Lowden* 7 and Laguna Catemaco, *Lowden* 9. Guatemala: Dept. Izabal, Quirigua, *Lowden* 10 and Puerto Barrios, *Lowden* 11. Honduras: Dept. Cortes, Puerto Cortes, *Lowden* 13 and 13.5 miles inland from Puerto Cortes *Lowden* 14; Dept. Atlantida, Tela, *Lowden* 15 and Santiago, 11 miles W of Tela, *Lowden* 16.
P. parviflora	8	Panama: Province Herrera, Los Llanos de Santa Maria, *Lowden* 20; Province Panama, between Chepo and Pacora, 7 miles from Chepo, *Lowden* 21.
subg. *Reussia*		
P. rotundifolia	16	Honduras: Dept. Comayagua, Lago Yojoa, Pito Solo, *Lowden* 12. Nicaragua: Dept. Granada, near Granada, *Lowden* 17, 18. Costa Rica: Province Guanacaste, 1 km. from Arenal, 2 km. from Trenadora, *Lowden* 19. El Salvador: Dept. La Liberatad, Laguna Zapotitan, *Lowden* 23.

Table 3. Spot Colors of Phenolic Compounds in *Pontederia* and Related Genera

Spot #	*No Reagent* Visible Light	*No Reagent* UV Light	*Reagent* NH4OH UV Light
1		aqua	green (in part)
2		aqua	green (in part)
3		purple	yellow green brown (in part)
4		cream-yellow	
5		blue purple	
6		green blue-cream purple	
7		white blue	
8		aqua	
9		dark blue	
10		aqua	green (sometimes)
11a		rose cream	
11b		blue green-pale blue	
11c		blue purple	
12	green brown	green yellow, red brown-pink purple	
13	green brown	pink purple-bright pink	
14		purple, blue-white blue	
15a		yellow green brown	
15b		yellow	
16	pink (sometimes)	bright-dull pink	
17		purple	
18		dull green blue-purple	
19		dull pink	
20		dull yellow green brown-green blue	
21		salmon	
22		yellow green brown	
23		yellow-gray cream	
24		pale blue	
25		dark yellow green brown	
26		dull pink purple	

Table 4. Summary of Spot Occurrence of Phenolic Compounds in *Pontederia* and Related Genera[2]

Taxon	Spot # 1	2	3	4	5	6	7	8	9	10	11a	11b	11c	12	13
Pontederia cordata var. *cordata*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Pontederia cordata var. *lancifolia*	+	+	+	+	+	+	+	+	+	+	+			+	+
Pontederia cordata var. *ovalis*	+	+	+	+	+		+	+	+			+		+	+
Pontederia sagittata	+	+	+	+		+	+	+	+	+	+	+	+	+	+
Pontederia parviflora	+	+	+	+	+	+	+	+	+	+	+		+	+	+
Pontederia rotundifolia	+	+	+	+	+	+	+	+	+	+	+			+	+
Heteranthera limosa	+			+		+	+	+	+	+				+	+
Eichornia crassipes	+	+	+	+			+	+	+	+	+			+	+

[2]A + sign represents the presence of phenolic compounds based on position and color of spot on chromatograms. *Eichhornia* and *Heteranthera* vouchers are: *E. crassipes*, Mexico, State Vera Cruz, Carretera Nacional 180, El Puente de Teculapilla, 5 km NW of Lerdo, *Lowden* 41 (OS); *E. crassipes*, El Salvador, Lago Illopango, W side of Apulo, *Lowden* 39 (OS) & Honduras, Lago Yojoa, Pito Solo, *Lowden* 40 (OS); *H. limosa*, Panama, Province Herrera, Los Llanos de Santa Maria, *Lowden* 38 (OS).

Table 4. (cont.)

Taxon	14	15a	15b	16	17	18	19	20	21	22	23	24	25	26	Sample Size
Pontederia cordata var. *cordata*	+	+	+	+	+	+	+	+	+		+	+	+		77
Pontederia cordata var. *lancifolia*		+		+							+		+		4
Pontederia cordata var. *ovalis*	+				+			+							1
Pontederia sagittata	+	+		+		+	+	+		+	+	+	+	+	100
Pontederia parviflora	+			+				+				+	+		37
Pontederia rotundifolia	+			+	+		+	+				+	+	+	86
Heteranthera limosa				+		+							+		3
Eichornia crassipes				+			+	+	+						3

AN UNUSUAL SUBSTRATE FOR POLYSIPHONIA PANICULATA MONTAGNE. Once in a while the curious juxtaposition of circumstances leads to an unusual find. Such a situation occurred during the summer of 1972 when we were exploring the algal communities along the edge of the San Andreas fault, at one of its drowned points. The fault emerges from a land position to follow Tomales Bay some 60 miles northwest of San Francisco. From Tomales Bay the fault lies under Bodega Bay and across Bodega Head, still on a northwesterly line.

We were engaged in field work for the Pacific Marine Station at Dillon Beach, California, and while working the mud flats along the east side of Tomales Bay at a place known as Lawson's Landing came across a rather curious partnership. Here we found a presumably symbiotic partnership between the rhodophycean alga *Polysiphonia paniculata* Montagne and the Horseneck Clam, *Tresus nuttalli* Conrad.

At the time we were collecting macroalgae, various species of *Ulva* being very common on the flats, and as we examined a stand of *Zostera marina* L. in a shallow subtidal area, we found individual plants of *Polysiphonia paniculata* scattered throughout the *Zostera.* Upon grasping the alga it became readily apparent that something unusual was occurring, because the alga would quite noticeably retract into the mud. Small plants would actually vanish from sight, going to depths that made any attempt to collect them futile. The first samples we collected of the alga lacked the lower portions.

Further search among the Zostera revealed another movement; whenever several hunters gathered around one of the *Polysiphonia* plants, it would "settle" downward several centimeters, almost as if it were anticipating our next action. Never having had algae attempt to "get away" before, we concentrated on solving the mystery. After several more misses, we succeeded in getting a whole plant, the trick being for one person to stalk the plant, and moving carefully, to use a long bladed knife to cut through the mud as deeply as possible below the protruding portion of the plant as the grab for the plant was made.

The cut brought to light a portion of the substrate to which the *Polysiphonia* was attached, and it proved to be the distal portion of the siphon of *Tresus nuttalli.* That the alga was firmly attached to the siphon was quite apparent, and subsequent microscopic examination revealed that the prostrate branches of the *Polysiphonia* had penetrated into the epidermal tissue of the siphon to a depth of several millimeters. Most of the samples we obtained in this manner were evidently from older clams, being 2 plus centimeters in the longest dimension.

Our examination of the general area suggested that the *Polysiphonia* serves to hide the siphon from overhead observation, thus affording some degree of protection to the clam. At no time were we able to see a protruding siphon or any evidence that a siphon was present, although the alga was very evident. We collected during low tide periods, and this did not coincide with the clam's feeding times. As far as we were able to determine over the several acres of flats, the association was confined to the stands of *Zostera.* On the open areas of the flats, heavily dug over by clam diggers, only siphons or siphon holes were to be seen.

We were unable to determine the significance of the association other than on an inferential basis. Generally in this region *Polysiphonia* can be regularly found wherever a firm substrate and tidal flow can be paired. It seemed logical to us that the clam benefited from the position of the alga, and that the alga would in turn benefit from the flow of water into and out of the siphon of the clam. This flow certainly would provide a source of nutrients better than the usual rock or wharf substrate.

A search among specimens in the herbarium at the Station revealed that previous collections of *Polysiphonia* had been made in the same mud flat area, but there was no reference to the type of substrate from which these previous collections were made. Due to the lack of any